THE FRUIT OF OPUNTIA FULGIDA

A STUDY OF PERENNATION AND PROLIFERATION IN THE FRUITS OF CERTAIN CACTACEÆ

BY

DUNCAN S. JOHNSON

PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON
WASHINGTON, 1918

CARNEGIE INSTITUTION OF WASHINGTON
PUBLICATION NO. 269
15075
The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

CONTENTS.

	PAGE
Comparison of the fruit of *Opuntia fulgida* with those of other angiosperms	5
Vegetative structure of *Opuntia fulgida*	8
Reproductive organs of *Opuntia fulgida*	9
Origin and structure of the flower	9
Development of the wall of the ovary with its tubercles	9
Structure and fate of the leaves of the ovarian wall	10
Areoles or axillary buds of the ovarian wall	11
Number, size and distribution of the areoles	12
Origin of the growing point of the areole and sequence of initiation of its organs	12
The trichomes of the areole	13
The nectaries of the areole, their distribution and morphology	14
Spines or thorns of the areole, their distribution, structure, and fate	15
Bristles or spicules of the areole, their number, structure, and fate	16
The perianth, stamens, style, and stigmas, their development and abscission	17
Morphology of the ovary	20
The fruit: Its structure, persistence, and fate, normal and abnormal	25
The fruit at the time of abscission of the perianth	25
The mature fruit	27
The perennating fruit: Its structure and secondary growth	29
The seed: Its structure, persistence, and germination	32
Proliferation of flower and fruit	35
Proliferation from attached flower buds	35
Proliferation of persistent attached fruits	37
Proliferation of fallen fruits	38
Causes and significance of perennation and of the diverse types of proliferation	41
Proliferation of flower or fruit in allied species	47
Proliferation of joints and fruits in relation to the sterility of fruits	51
Summary and conclusions	53
Literature cited	56
Explanation of plates	57

A mature plant of *Opuntia fulgida* on reservation of Desert Laboratory at Tucson, showing a frequent type of forked trunk, due to injury of main axis, also the branching habit and clusters of fruit. The nesting bird is the cactus wren, *Heleodytes brunneicapillus couesi* (Sharpe).

THE FRUIT OF OPUNTIA FULGIDA.

A STUDY OF PERENNATION AND PROLIFERATION IN THE FRUITS OF CERTAIN CACTACEÆ.[1]

By DUNCAN S. JOHNSON.

This paper embodies a discussion of the occurrence and significance of a number of striking peculiarities in the development and fate of the persistent, self-propagating fruits of certain opuntias. The discussion will be concerned primarily with the perennation and vegetative propagation of the ovary of *Opuntia fulgida*. This cactus has been chosen for special consideration because of its most remarkable power of budding off secondary flowers from the primary ones and also of forming new flowers and vegetative shoots from the long-persistent fruits.

This investigation has been aided by grants from the Department of Botanical Research of the Carnegie Institution of Washington. Acknowledgment is here made to Director D. T. MacDougal for making available to the writer the facilities of the Desert Laboratory at Tucson, Arizona, and of the Coastal Laboratory at Carmel, California. The principal parts of the work have been done at these two laboratories. Other portions of it and much of the writing of this paper have been done at the Harpswell Laboratory, at South Harpswell, Maine, and at Johns Hopkins University. Acknowledgment is also made, for aid in securing material, information, or photographs for this study, to Drs. Forrest Shreve and Hermann Spoehr, of the Department of Botanical Research of the Carnegie Institution, to Dr. David Griffiths, of the Bureau of Plant Industry, United States Department of Agriculture, to Dr. J. N. Rose, of the Smithsonian Institution, and to Dr. N. L. Britton, of the New York Botanical Garden.

COMPARISON OF THE FRUIT OF OPUNTIA FULGIDA WITH THOSE OF OTHER ANGIOSPERMS.

One of the almost universal characteristics of the fruit in angiosperms is the comparative brevity of its development. The whole duration of this, from the inception of the flower to the ripening of the fruit and its final separation from the parent plant, or its opening for the discharge of its seeds, is usually less than a year, often very much less.

The phases of this developmental cycle of the fruit which can usually be distinguished are: First, a period of initiation and maturing of the parts of the flower, which opens for pollination at about the time an egg has been

[1] Botanical contribution from The Johns Hopkins University, No. 56.

formed in the embryo sac; secondly, there follows soon after pollination, which is usually succeeded by fertilization, a period of active vegetative growth of the ovary and often of other parts which are to enter into the make-up of the fruit. While the fruit is thus growing to its mature size the seeds are also taking on their characteristic form and size. Thirdly, accompanying or immediately succeeding the final maturing of the seeds, a process of ripening occurs in the fruit. During this ripening process the outer tissues, the mesocarp and epicarp of the fruit, may soften to form a juicy pulp. In this case the starches, distasteful glucosides, acids, tannins, alkaloids, etc., which are often present in the cells of this pulp in the green fruit, are transformed into the sugars, mild acids, and other tasteful flavors, and often also into brightly colored glucosides that make the fruits attractive to animals. While these changes are taking place in the outer layers of the fruit the inner layer, the endocarp, may harden to form the firm stone that protects the seed when it is eaten by animals. In other types of fruits, as in pods and capsules, the ripening process involves a drying out and hardening of all the tissues of the fruit.

Ripening of the fruit is usually followed, often very promptly, by its separation from the plant or by its dehiscence and the discharge of its seeds. Either of these two fates of the fruit involves the more or less immediate death of its tissues, aside from the seeds. In a few fruits, such as that of palms like the coconut or the pomes of the Rosaceæ, certain tissues of the fruit may remain alive for some weeks or months after separation from the parent plant. The growth occurring in these cases is, however, comparatively slight and it does not give rise to new buds or new plants.

In the cases of certain opuntias, chiefly cylindropuntias, the fruits differ from the usual type characterized above in several very remarkable particulars. In the first place the fruits do not ripen with the maturing of the seeds, but continue to grow actively without undergoing the usual softening and change of color and of chemical composition so characteristic of the ripening process of most fleshy fruits. Secondly, the fruits of *O. fulgida* are not shed from the plant when the seeds are ripe, but usually remain firmly attached and growing, year after year. Thirdly, these attached fruits (or even the unopened flowers), may, *in situ,* give rise from their axillary buds to from one to ten secondary flowers and fruits. A few weeks later these secondary flowers may give rise in the same way to tertiary ones and these in turn to quaternary ones. Thus, three or four generations of flowers and fruits may be produced, all in a single blooming season of three or four months. Fourthly, if the fruits become separated from the plant and fall on moist soil, the same axillary buds which in the attached fruits would form nothing but flowers will, in the fallen fruits, give rise to vegetative shoots and roots and to these only. Finally, the embryos of the ripe seeds, inclosed in the persistent, attached fruits, retain their power of germination for many years.

Certain of the peculiarities above noted in the fruits and seeds of *Opuntia* are, it is true, found in a few other plants, though in none of which the writer has found record is there such an aggregate of unusual features of development, and certain of these features are unknown outside the genus *Opuntia*.

The persistent attachment and continued growth of the fruit just noted is, as far as I can learn, recorded for but one other family of angiosperms, the Myrtaceæ. In the genera *Callistemon* and *Melaleuca*, for example, the fruits may persist for 10 or 15 years. In the former, according to Ewart (1907), the fruit opens and discharges the living seeds only when it has been killed by the cutting off of its water-supply. This latter may happen in consequence of severe drought, of the breaking off of the branch bearing it, or from the death of the branch or whole tree from fire or other cause.

There are, however, three important differences between the behavior of the fruits of this Australian "bottle-brush" tree and those of such opuntias as the "cholla" (*O. fulgida*). In the first place, the persistent fruit of *Callistemon* does not possess axillary buds and therefore does not, like *Opuntia*, give rise to secondary and tertiary flowers and fruits from these. Secondly, the fruits of the bottle-brush tree, though they may open and discharge their seeds with the first cutting off of the water-supply, do not themselves fall from the tree until some time after they are dead; hence, they can play no part in the vegetative propagation of the species. Thirdly, the seeds of *Callistemon* are ultimately shed from the fruit to play the most important rôle in the dissemination of the plant, while the seeds of the fleshy fruits of *Opuntia fulgida* are, as we have seen, never discharged and apparently rarely germinate under natural conditions.

From this comparison of the opuntias with the only other family of plants having fruits with similar peculiarities, it is clear that these Cactaceæ have become much more abnormal as regards the behavior of propagative structures than any other family of angiosperms. Moreover, the readiness with which a growing-point destined to give rise to a flower may be induced to form a vegetative shoot (by the mere separation of the fruit bearing it from the parent plant) suggests the possibility of discovering here some of the causes determining the production from the same meristematic mass, in one case of a reproductive organ or in another of a vegetative shoot.

With this much of suggestion of the structures and phenomena we are to deal with, we shall now examine more closely into the development and fate of the flower, fruit, and seed of certain opuntias. We shall be concerned primarily with those of *Opuntia fulgida*, in which these structures have been studied most carefully in Tucson, Carmel, and Baltimore. Incidentally we shall also note the structure and capacity for propagation of the vegetative joints of certain species, in order that we may compare with them the structures and phenomena observed in sprouting fruits.

VEGETATIVE STRUCTURE OF OPUNTIA FULGIDA.

Opuntia fulgida is a tree-like, Sonoran species of *Cylindropuntia,* which commonly grows to 2 or 3 meters in height and forms a rather irregular flat-topped crown. The older or main branches are horizontal, or ascendant at their bases, but bent down at their tips by the weight of the thick terminal branchlets and often of the large clusters of fruits (fig. 1). The spiny trunk is dark brown in color, woody in texture, and may reach 20 or 25 cm. in diameter. The main branches, which are woody like the trunk, may become 8 or 10 cm. in diameter. The ultimate branches at the end of the first season's growth are often 3 to 5 cm. in diameter and 15 to 25 cm. long. These younger branches taper abruptly at the ends and the lateral surfaces are provided with prominent and somewhat elongated mammillæ or tubercles (figs. 4, 5, 9*a*). Each tubercle, at this time, bears at its upper end from 7 to 12 sheathed spines and the growing-point of a lateral bud (figs. 4, 9*b*). The number of spines in each areole steadily increases with age, and hence a branch 10 years old may bear 50 spines in each areole. The leaf to which the areole is axillary is a small and very transient structure which (on falling) leaves only a minute scar, like that to be seen on the fruit (figs. 5, 47). The vascular system of the stem is net-like in arrangement, being of the same general type as that described and figured by Ganong (1894, fig. 7). During the first year the bulk of the new joint is made up of the mucilaginous pulp of the pith and cortex. The latter has a well-developed photosynthetic and aerating system of the type to be described in dealing with the fruit, and large numbers of slime-cells (*cf.* Wetterwald, 1889, fig. 19). Chloroplasts are abundant throughout the whole thickness of the cortex of the stem and may even occur within the zone of woody bundles, as happens in the projecting tubercles. With the increase in thickness of the branch the woody cylinder seems to grow in diameter more rapidly than the fleshy cortex. The latter finally becomes stretched and smoothed out and the cortex of the mature stem is comparatively thin and dry (fig. 2, at base).

On some plants of this species, as has been noted by Toumey (1895), certain of the new joints may remain relatively short and have less prominent tubercles and fewer spines, becoming thus rather fruit-like in form (fig. 7*a*). These joints are readily detached and on moist soil may give rise to new plants by proliferation, just as the ordinary vegetative branches of this and many other opuntias may do.

REPRODUCTIVE ORGANS OF OPUNTIA FULGIDA.

The reproductive structures (flower, fruit, and seed) to which most attention has been paid in this study, will be described in some detail under three captions: (1) the origin and structure of the flower; (2) the fruit, its structure, persistence, and fate, normal and abnormal; (3) the seed, its structure, persistence, and germination.

The most aberrant features of the development of these reproductive organs are: the structure of the wall of the submerged ovary, with its numerous axillary buds; the capacity of these buds to initiate secondary flowers, either immediately before the primary ones are open or later, in the same or succeeding seasons; and finally the ability of these same axillary buds, when the fruit is detached, to form adventitious roots and shoots and thus to initiate new plants.

ORIGIN AND STRUCTURE OF THE FLOWER.

The primary flower of the season in *Opuntia fulgida* arises from one of the upper or more terminal axillary buds or areoles of a last year's vegetative joint or from an areole of a fruit of the first, second, or third year preceding. The number of flowers developed on any one joint or fruit in a single season ranges from 1 to 5 or more (figs. 4, 9*a*). In the case of the fruits, flowers may be formed from other areoles in succeeding years until as many as 10 or 12 flowers and fruits are often found attached to a single persistent fruit (fig. 48). The primary flowers of a season are first evident, in *O. fulgida* growing near Tucson, during the latter half of April. Open flowers are rarely seen before the middle of May. The first flowers to appear and to open are those developed on vegetative branches. In early May 1912, the larger flower-buds on vegetative branches of one plant observed were 21 mm. long, while the longest ones on a persistent fruit of the same plant were but 7 mm. New flowers continue to open successively all through the summer up to the middle of September. (See Toumey, 1898; Lloyd, 1907).

DEVELOPMENT OF THE WALL OF THE OVARY WITH ITS TUBERCLES.

The very young flower-bud, when first pushing out of the tuft of trichomes and spicules of the areole, is a rather hemispherical body about 0.3 mm. in diameter. Its dome-like or somewhat conical upper end is formed by the few earlier of the 15 to 30 or sometimes 40 leaves that are finally developed from the wall of each ovary (figs. 4, 9*a*, 47). These leaves, when first formed, arch over the dome-shaped growing-point (figs. 13, 14). As the flower grows, the earlier leaves are pushed outward by the younger ones arising between them (figs. 17, 22). The axis of the flower becomes elongated to 1½ times its diameter and its surface becomes very irregular. Below each leaf and its associated bud the surface of the wall of the ovary protrudes to form a prominent tubercle or mammilla (figs. 14, 16, 20). This tubercle is at first finger-like; later it projects farthest at its upper end and

narrows to nothing at its lower end, giving it thus a rather triangular outline in a radial section of the fruit (figs. 4, 17, 28).

At the time of the opening of the flower these tubercles are from 6 to 10 mm. in length, are 4 or 5 mm. wide, and project 2 or 3 mm. at the top. In the younger flower-bud the radial width of the tubercle is greater in proportion to its length, longitudinal to the ovary, than is indicated above, while in the mature fruit the projection is much less. In morphological nature, this tubercle of the opuntias, as has been shown by Goebel (1889, p. 79), is the combined product of the growing upward together of the leaf-base and the axillary bud above it. This is clearly indicated by a comparison of different stages in its development (figs. 12, 14, 15, 17). The upper end of the tubercle is somewhat circular in cross-section (figs. 30, 49), and somewhat raised at the margin (figs. 21, 22; *cf.* also, Wetterwald, 1889, fig. 19). At the highest point of the abaxial side of the margin is borne the leaf, while the most depressed central portion of the end of the tubercle is occupied by the flattish growing-point of the axillary bud, which is surrounded by the rudiments of trichomes, spicules, and nectaries developed from it (figs. 9*b*, 12, 15, 32, 50). It is difficult to see how all the structures above *a*, at the left of the growing-point in figure 50, can be regarded as parts of a single leaf, as they apparently would have to be if the view of the morphology of the tubercle held by Darbishire (1904, p. 395) were accepted.

The growing-point of the flower, like that of the vegetative shoot, may be slightly convex in form during the period of the initiation of the wall of the ovary with its tubercles and the leaves borne by them. It may even retain some of this convexity during the initiation of the 16 or more sepals and petals (figs. 12, 13, 14). With the beginning of formation of the stamens and carpels, however, the same growing-point becomes depressed to form a cup narrowing in at the upper margin, about which the numerous (250) stamens are initiated. Later still, the margin closes in to form the carpels, which unite above to form the roof of the ovary, and finally stretch upward to form the style and its 6 stigmas (figs. 15, 16, 17).

STRUCTURE AND FATE OF THE LEAVES OF THE OVARIAN WALL.

The leaves of the wall of the ovary are, as noted, about 15 to 40 in number. Each leaf is approximately conical in form, has a slightly flattened base, and is curved inward above to end in a sharply pointed tip (figs. 4, 5, 11, 19, 23, 47). The mature leaf of the ovary is only 3 or 4 mm. long and but 1 or 1.5 mm. in diameter. It is abruptly constricted at the base to a stalk, which is nearer the ventral side and is barely a third the diameter of the part of the leaf just above (figs. 19, 50). The leaves of the lower third of the ovary do not attain more than half the size mentioned, while those of the upper quarter, which are more or less appressed against the sepals, may be somewhat longer and are commonly very much broadened (figs. 23, 47, at right). Before the ovary has reached half the size it attains at the opening of the

flower, the lowermost of the 15 to 40 leaves of the ovary have dropped off, many of them withering while mere rudiments, half-grown or less (fig. 20, lower areole). The separation occurs at the constriction mentioned, and by the time the flower is well opened all its leaves outside the calyx have fallen. This separation is apparently not determined by a definite abscission layer. The dropping of the leaf is followed by the shrinking together of the short stump of the leaf-stalk and later by the formation of a protecting scar-tissue of 15 to 20 layers of corky cells (fig. 14). Evidently these leaves of the wall of the ovary, being relatively few, small, and transient, are able, like the similar leaves of the vegetative joint, to play only a very subordinate part in the photosynthetic work of the plant. They are certainly much less important in this work than the abundant and permanent photosynthetic tissue of the wall itself.

In correspondence with this relatively unimportant photosynthetic work of the leaf, its internal structure shows little of the characteristic specialization of an efficient starch-making organ (figs. 45, 46). Stomata are few and scattered, on the under side of the leaf only. Instead of the characteristic palisade found in the leaves of most other plants and in the joints and fruits of *Opuntia fulgida* itself, we find the whole outer region, especially on the dorsal side of this leaf, made up of nearly isodiametric cells, among which are scattered small cells containing calcium oxalate crystals and much larger cells filled with slime or mucilage. The latter are of the type that will be described in more detail when we come to the consideration of the internal structure of the fruit (figs. 45, 46). Near the flattened base of the leaf (fig. 45), five vascular bundles are to be seen in its cross-section, but only the middle one of these reaches to the tip of the leaf. The subordinate, lateral bundles are made up chiefly of short, broad, thick-walled elements which are often oriented transversely to the leaf. The principal (median) bundle also includes many of these elements at its upper end, but has a larger proportion of more elongated tracheal elements in its lower portion (figs. 45, 56).

AREOLES OR AXILLARY BUDS OF THE OVARY.

By far the most significant peculiarity in structure of the wall of the ovary in *Opuntia fulgida,* as compared with other angiosperms, is the presence of the axillary buds or areoles distributed over its surface. There is one of these within the leaf, or its scar, at the top of each tubercle, though the basal ones of each fruit remain very rudimentary and never, as far as discovered, give rise to any structures other than a few small spicules or an occasional adventitious root on fruits fallen to the ground. What makes these axillary buds or areoles of the fruits of prime significance in the life of the plant is the fact that those at least of the upper two-thirds of the fruit remain active and each capable of giving rise, on the attached fruit, to a secondary flower or fruit. Or, if the fruit be detached from the plant, these areoles may give rise to adventitious roots and to vegetative shoots, thus initiating new plants.

The facts and structures of interest in connection with these areoles are: their number and distribution, the origin of the growing-point, the trichomes, the nectaries, the spines, and the bristles or spicules.

NUMBER, SIZE, AND DISTRIBUTION OF THE AREOLES.

Since there is a bud in the axil of each of the leaves of the wall of the ovary, except in the cases of 4 or 5 of the upper ones that are appressed against the sepals, the total number of areoles formed is nearly the same as that of the leaves. Mature ovaries show from 15 to 35 or (in joint-fruits) even 40 areoles. But these are not by any means alike in size or in the number of organs or organ rudiments present in them. The size varies from 1.5 to 3 mm. in diameter in flowers just opening, while the areoles of a three-year old fruit may become 4 or 5 mm. broad by 6 or 8 mm. long (figs. 4, 8, 47, 49). The areoles of the upper third of the fruit are in general larger and more complexly organized, while those of the lower third are usually much smaller and of very simple structure. The former are the ones most likely, under satisfactory conditions, to develop further. The lower ones usually grow little after the maturing of the fruit. They gradually become depressed more and more deeply into the surface of the fruit, till they are nearly buried from sight. The lower half-dozen areoles have never been seen to give rise to either flowers or vegetative branches. In a fallen fruit, however, adventitious roots may push out the upper border of such a dormant or apparently dead areole (fig. 100).

As seen from without, the mature areole appears as a grayish yellow, bulging cushion, of circular or somewhat longitudinally elongated outline (figs. 4, 8, 47). The surface of this cushion is made up of the ends of hundreds of spirally striated trichomes, which at first surround and overtop all other rudiments in the areole. In slightly advanced areoles dozens or scores of straight, barbed bristles or glochidia push from beside or beneath the tuft of trichomes in the apical half of the areole. Near the middle of such a cushion may be seen the flattish tops of one or several spine-tipped nectaries (figs. 14, 47, 48, 49, 50). Still later, in certain of the areoles of the upper third of the ovary, the tip of the bud of a secondary flower may be seen. This is at first covered by a protecting lattice made up of the peg-like leaves, which push out of the cushion of trichomes, just below the crescentic group of spicules and just above the nectary or nectaries of the areole (figs. 13, 15, 47). In the lower areoles of some of the more elongated fruits one or two spines may be formed which resemble those found in the areoles of the vegetative joints, but are usually weaker (figs. 13, 28).

ORIGIN OF THE GROWING-POINT OF THE AREOLE AND THE ORDER OF INITIATION OF ITS ORGANS.

The growing-point of the areole becomes distinguishable at a time when the subtending leaf has attained less than a quarter of its mature length; that is, when it is only 0.5 mm. long. It at first consists of a very small

group of more darkly staining cells, located in the very axil of the young leaf (figs. 12 at *x*, 14 at *x*, 16). With the further growth of the base of the leaf the supporting portion of the stem and the tissue derived from the axillary bud itself together push outward and upward (see Goebel, 1889, p. 79) to form the young tubercle or mammilla (figs. 14, 15, 50). This combination structure grows more rapidly on the outer side, with the result that the growing-point of the areole comes to lie on the inner face of the tubercle (fig. 14). This shoot apex forms a slightly bulging dome of about half the length of the tubercle and facing directly toward the growing apex of the flower (fig. 14). Later, by the growth of the tissues and organs arising from the adaxial side of the growing-point, the upper end of the tubercle becomes directed more outwardly, often at an angle of 45° with the axis of the flower (figs. 15, 17, 19). The growing-point of the areole from this time onward faces almost directly upward (figs. 12, 17, 20, 24).

The first rudiments to appear on the growing-point of the new axillary bud are the monosiphonous trichomes, which arise on the margin next the leaf. Following these trichomes there appears a nectary and more trichomes, on the same side, and later another series of trichomes on the opposite or inner margin of the growing-point (figs. 12, 17).

TRICHOMES OF THE AREOLE.

The first organs to be developed in the areole, after the growing-point itself, are, as noted above, the monosiphonous trichomes. These are developed in large numbers, scores or hundreds, by the proliferation of many adjoining superficial cells about the growing-point. At first they appear around half the circumference of the growing-point on the side next the subtending leaf (figs. 17, 32, 50). Soon afterward others appear, in smaller numbers, on the side of the growing-point next the main axis. When still later a group of spicules appears on this side of the growing-point, and successive nectaries on the abaxial side, both sorts of structures are surrounded, and more or less hidden, by the masses of trichomes developed about them. The youngest trichomes, when 3 or 4 cells long, are bent over the growing-point (figs. 10, 50). Later, when they attain their mature length of 8 or 10 cells, they stand up nearly perpendicularly about the growing-point, though they may (especially in the upper portion) become considerably bent or kinked (figs. 50, 51). The mature trichome consists of a single row of from 6 to 10 or 12 cells. It is about 10 or 12 microns in diameter at the base and three or four times this at the top. The basal cells of the trichome are usually cylindrical, with thin, smooth walls, while the upper 3 or 4 cells are often barrel-shaped and have thickened, spirally marked walls (figs. 51, 52). The terminal cell is often oval, with the smaller end upward. In the older trichomes one or more of the terminal cells may have fallen off, leaving the hair with a square end, commonly the open end of an empty dead cell.

There can be no doubt that these trichomes serve to protect from desiccation the growing-point of the areole and the young rudiments formed by it. In other words, they serve the function served by bud-scales, or modified leaves, in the axillary buds of most woody plants. The number and length of these trichomes enables them completely to submerge all other structures in the bud except the nectaries and the full-grown spicules. The latter protrude for half their length, while the flat ends of the former can be seen in surface view of the areole, each with a densely packed ring of trichomes about it that have been crowded aside by the swelling of the nectary. These clustered trichomes make a more effective protection also because of the enlarged, thick-walled cells at the end of each of them. The lattice-like thickening of these cells enables them to maintain their form and full size when dried out completely by the desiccating winds of their native habitat. Whether the trichomes have other functions at any other period of their existence has not been determined. None has suggested itself to the writer as probable in the course of this study.

The final fate of these trichomes has been suggested by what was said of the breaking-off of the terminal cells. This process is apparently repeated until the trichome practically disappears; at least, the older areoles contain large numbers of decapitated hairs, many of them with only a few of the basal cells left.

NECTARIES OF THE AREOLE: THEIR DISTRIBUTION AND MORPHOLOGY.

In every areole, soon after the differentiation of its growing-point and the development of a few score of trichomes, there appears among the latter, on the side of the growing-point toward the leaf, the rudiment of a nectary. In many of the smaller, basal areoles of the fruit only one or two of these nectaries may be formed, and these lie close to the sagittal plane of the areole (figs. 24, 47). In the larger, upper areoles, however, the number of nectaries may continue to increase with the growth of the areole until, by the end of the first growing-season, there may be 8 or 10 nectaries present in each (figs. 5, 47, 48, 49). As the areole grows year after year on the persistent fruit, the number of living and withered nectaries may continue to increase till 20 or more have been formed. Not more than 4 or 5 mature, living nectaries are present at one time, but a number of younger ones may be initiated between a mature one and the growing-point before this begins to shrivel. In the upper areoles of a primary ovary secondary flower-buds usually appear after but 2 or 3 nectaries have been developed, and these are soon crowded aside to wither as the secondary bud swells (figs. 47, 49). In case secondary flowers are not formed from an areole until the second or a later year, there may be many old nectaries found crowded aside or partially crushed by the stalk of the enlarging secondary fruit (fig. 14). These nectaries were evidently initiated before the flower, since the latter, as we have seen, involves the whole growing-point of the areole (figs. 10, 12, 14).

The youngest stage of the nectary seen was a low, conical projection of the superficial layers of the meristem among the trichomes immediately beside (abaxial to) the growing-point of the areole (figs. 12, 50). Very soon a small vascular strand is differentiated, just below the base of the nectary, which later penetrates a short distance into it (figs. 50, 56). As the nectary grows it widens somewhat near the top and becomes more or less constricted at the base (fig. 17). When mature, the stalk of the nectary has about three-fifths the diameter of its upper half. The top usually has a small depression with a small tubercle at its center (figs. 17, 20). Sometimes this tubercle develops to a well-marked spine (fig. 23). These facts clearly indicate, as has been noted by Ganong (1894, p. 59), that the nectary is homologous with the spines that are so abundant on the joints of many opuntias, but are often wanting on their fruits. The steady increase in number of the nectaries is therefore strictly comparable with the constant increase in number of the spines of the areole of the vegetative joint (*cf.* p. 8).

The epidermis of the mature nectary is small-celled and thin-walled, except at the top and on the spine or tubercle itself. Here the cells are small and irregularly compacted and their walls are provided with a cutin layer several microns in thickness, which peels off rather readily (fig. 56). The cells of the interior of the nectary seem to be little differentiated, except for the occasional trace of a vascular bundle near the base. They are often longitudinally elongated to 10 or 12 times their diameter and are commonly pointed at both ends (fig. 56). Most of these cells in the mature nectary have darkly staining protoplasts and nuclei, but a considerable number of them are nearly devoid of contents except for a large, stellate crystal of calcium oxalate.

The mature nectary remains plump and probably active for one growing season and then, as has been suggested, it gradually withers and dries up to a shriveled brown rod of scarcely a tenth the diameter of the functional nectary. It is this shriveled mummy that persists indefinitely, year after year, among the trichomes of the areole (fig. 14).

SPINES OR THORNS OF THE AREOLE: THEIR DISTRIBUTION, STRUCTURE, AND FATE.

While spines, to the number of 6 or 8 and of a length of 3 or 4 cm., are present in areoles of the vegetative joint of *Opuntia fulgida*, they are usually wanting from the fruits (*cf.* Wetterwald, 1889, fig. 18). When spines do occur in a fruit there is usually but a single spine in each of only a few of its areoles (figs. 7*b*, 7*c*). The position of this spine is essentially that of the first nectary of the more normal fruits; that is, it stands in the sagittal plane of the areole, just within the subtending leaf.

The structure of these spines may be described briefly here, leaving the fuller discussion of this and their development for a later paper in which it is planned to deal more in detail with the stem. The spines initiated on the fruit seldom attain the size and strength of those on the stem. They also

often drop off with the maturing of the fruit, apparently in consequence of the withering of the base of the spine. The number of spines in the spine-bearing areoles of the joint-like fruits evidently increases, from year to year, much as in the areoles of the stem.

Each spine consists of a slender, barbed axis or core and a glistening white, striated sheath. The surface cells of the core, in the upper half of its length, project outward and downward at the tip to form the extremely sharp retrorse barbs (figs. 53, 54). The sheath, which at first covers the whole core of the spine with a tightly fitting jacket, is made up of several layers of greatly elongated and very thick-walled cells (figs. 54, 55). As the spine matures it shrinks in diameter and separates from the sheath. The latter at the same time contracts longitudinally, so that its tip is punctured by the point of the spine. Later the basal portion of the sheath splits to several strips, which are soon folded back on themselves in loops (fig. 53). The result of this is that the tips, even of spines developed in the greenhouse, are left naked for several millimeters.

BRISTLES OR SPICULES OF THE AREOLE: THEIR NUMBER, STRUCTURE, AND FATE.

On the inner or abaxial margin of each areole there is a crescentic group of barbed, yellow, weak-based bristles, which form the only armament of most fruits of this species. This curved cluster of spicules reaches about one-third way around the growing-point of the areole (figs. 32, 50). The tips of the older bristles lie close against the surface of the ovary just above the areole. Each individual bristle is practically straight, about 50 or 60 microns in diameter and 1 to 1.5 mm. long. The surface of the bristle is made up of thick, yellow-walled cells 5 to 8 microns broad by 100 microns long. The outer ends of these cells project slightly outward and sharply downward to form the characteristic barbs which make these bristles such a persistent and irritating reminder of an encounter with the fruits or joints of this cactus (figs. 57, 58). The cells of the interior of the bristles are of slightly smaller diameter, more elongated, with clear and much thinner walls (figs. 58, 59).

The bristles are the last of the several types of organs to appear in the areole. Even the first of them do not appear till scores of trichomes and one or two nectaries have been developed (figs. 12, 50). The rudiment of the bristle is not, like that of the trichome, of a single row of cells, but is 5 or 6 cells across when it first pushes out from the growing-point (fig. 56). The number of bristles in an areole increases with age. At the time the leaf is shed the crescentic cluster about the growing-point may consist of 6 or 8 concentric rows of 20 to 30 bristles in each row (figs. 32, 50). In the sterile areole of a four-year-old fruit this number may be double or triple that just mentioned. When once formed the bristles evidently persist indefinitely unless dislodged by browsing animals or by the development of a flower or shoot from the areole. The absorption of a growing-point in the production of such a flower or shoot of course puts a stop to the appearance of further bristles from that areole.

PERIANTH, STAMENS, STYLE, AND STIGMA: THEIR DEVELOPMENT AND ABSCISSION.

The order of initiation of the organs of the flower is an acropetal one. The series begins with the formation of the peg-like leaves, followed by that of the areoles, the sepals, and petals, all from the characteristic convex growing-point like that of the stem. Then with a change in the growing-point to a concave, cup-like shape, the series of floral parts is completed with the initiation of the stamens and carpels, or perhaps we should say with that of the placentas and ovules, which are formed deep in the bottom of the cup (*cf.* also Goebel, 1886).

The perianth of *Opuntia fulgida* consists of about 8 sepals, light green in color, and of a like number of petals, rose-pink in color. These sepals and petals are initiated about the growing-point in the same way that the leaves of the ovary are, but differ from the latter in the important particular that no axillary buds are developed at the bases of the perianth members and that there is no tubercle formed at the base of either sepal or petal (figs. 17, 22, 47). In mature structure also the perianth divisions differ strikingly from mature leaves. Even the sepals are considerably broader and flatter than the leaves, with more vascular bundles, while the obovate petals are very broad and have a far more complex, reticulate vascular system than the leaves (figs. 47, 64). The mature perianth opens after midday (in mid-afternoon according to Lloyd, 1907). It forms a saucer-shaped flower an inch or more across. A few days after opening the whole perianth falls off, set free by the formation of a well-defined abscission layer.

The 250 stamens of the flower have filaments about 2 or 3 times as long as the anthers. Each stamen arises as a dome-like elevation, 6 or 7 cells in diameter, on the margin of the now concave growing-point (figs. 16, 18). As the stamens develop they bend inward over the growing-point, the youngest ones standing nearly at right angles to the axis of the flower (figs. 17, 20). Later they swell at the end, as the microsporangia appear, and gradually become more erect, but not completely so until the flower is open (figs. 22, 23, 61).

The internal development of the microsporangia is apparently not essentially different from that of the typical angiosperm. The upper, older stamens open first, as they dry out first. The pollen-grains are irregularly globular, with a yellowish, pitted exine of about 4 or 5 microns in thickness, and of a columnar or palisade-like structure when seen in optical section.

The carpels, the last structures of the flower to be formed, are 6 or sometimes 7 in number. This is clearly indicated by the number of rudiments of carpels initiated around the growing-point, by the number of lobes of the stigma, and by the number of placentas in the mature ovary (figs. 17, 31, 32, 33, 34). No case was observed with 5 carpels, the number found by Engelmann (1887) in the plants studied by him. The first rudiments of the carpels become evident after about 6 or 7 tiers of stamens have been devel-

oped; that is, when there are 6 or 7 stamens, one above the other, on one side of the growing-point in a single radial longitudinal section (fig. 18). The carpel rudiment at its initiation is twice as thick as that of a stamen. It differs, also, in that it almost immediately bends inward above the growing-point to meet its fellows and thus to complete the roof of the ovarian cavity (figs. 17, 18, 19). Soon after the tips of the carpels meet they begin to fuse together along their radial surfaces to form the rather stout style, which incloses a papilla-lined stylar canal, that is star-shaped in cross-section (figs. 21, 23, 35, 37). The very tips of the carpels, for a length of 3 or 4 times their diameter, remain unfused and form the stigmatic lobes. These finally become 1 to 1.5 mm. long and are densely clothed with swollen, sac-like hairs that serve for the attachment of pollen-grains (figs. 23, 36). Beginning at a depth of 5 or 6 layers inward from the wall of the stylar canal is a corrugated tube of conducting tissue 8 to 20 or even 30 cells in thickness, through which the pollen-tube is to push its way (figs. 22, 34, 35). The slender cells of this conducting layer extend upward to the very base of the hairs of the pollen-receiving surface of the stigma (fig. 36). At the base of the style this layer is continued downward as a series of strands reaching to the roof of the ovary (figs. 22, 23, 24). The mature stigma lobes are continued outward and downward to form the characteristic 6-rayed or 7-rayed structure seen in the open flower (figs. 30, 31). The lining of this part of the ovary wall, down to the uppermost ovules, is covered by slender hairs protruding into the cavity of the ovary. These probably help to conduct the pollen-tubes to the micropyles.

Not only do the carpellary lobes, which are at first transverse, grow upward after meeting above the depressed growing-point, but they may also often grow downward somewhat into the ovarian cavity, thus making the roof of the latter lowest near the center (figs. 11, 21, 61). Transverse sections of the ovary at this time may show several upward prolongations of the ovarian cavity, separated from each other by the downward growth of the carpels at the plane of juncture of the two carpels of each pair. The impression given by such a section is that of a compound ovary with 6 or 7 separate cavities.

The separation and fall of the perianth, and other parts that fall with it, is a complicated and rather variable process, as compared with the shedding of parts in most choripetalous flowers. In about 3 days after the flower has opened the withering of the sepals and petals has gone so far that all those of a flower are twisted together into a cone of dry, crisp remnants; that is, the parts of the flower do not drop off individually, as usually happens in choripetalous angiosperms, but the whole series of sepals, petals, stamens, and in some cases even the style, are cast off from the ovary at once, all attached to a cup-like common base stripped off from the upper end of the ovary. This wholesale shedding of the floral parts is accomplished by the formation of a highly developed abscission layer across the entire upper end

of the ovary. The form of this layer is not a simple transverse plane, but is that of an inverted cone, usually perforated at the apex. This funnel-shaped layer of tissue is initiated in cells 15 or 20 layers beneath the surface of the cup-like upper end of the ovary that bears the stamens, petals, and sepals (figs. 23, 58, 60, 61).

In a diametric longitudinal section of the ovary this abscission layer usually starts in at the base of perianth, either outside the sepals or, more rarely, between these and the petals. From here it extends downward, parallel to the surface of the cup at the top of the ovary, to a level just a little above the base of the style, where the abscission layer again comes out to the surface of this cup (figs. 23, 24, 60, 68). Less frequently the more or less developed abscission layer may extend across beneath the bottom of the cup at the top of the ovary. In this latter case the style is cut off, along with the stamens and perianth attached to the same complete, shriveled funnel (fig. 61). In the more usual case, first noted, the perianth and stamens only are borne on a shriveled funnel that is perforated at the base, while the style is shed separately, breaking across just above its base (fig. 24). In rarer cases, where the abscission layer starts in at the top within the perianth (fig. 23), the petals and sepals must evidently be cut off separately. Whether a real abscission layer is developed in each part or not was not determined.

The first origin of the abscission layer across the top of the ovary is evidenced by a swelling, chiefly a radial elongation, of a continuous layer of cells in the midst of the wall of the ovary, in the region stretching between the base of the perianth and the base of the style (figs. 61, 68). Apparently any cells along the line of the abscission layer to be may take part in its formation, except such specialized cells as those of the vascular bundle, the mucilage cells, and the crystal-holding cells. The cells that are to form the abscission layer increase in radial length to about twice their tangential diameter. Then the cells divide tangentially into two nearly isodiametric cells (figs. 67, 68). A further tangential division follows very soon in each of these cells, resulting in the formation of a row of 4 cells, of which the two middle ones have only half the radial thickness of the two outer (fig. 67). It is at this stage, or sometimes after one or two further tangential divisions, that abscission occurs. The details of possible changes in the radial walls of the abscission cells have not been studied. (See Lloyd, 1914, p. 70, and 1916, pp. 213-230). It is clear, however, that in consequence of the shrinking of the perianth, on drying, the delicate radial walls of the thin, tubular, cambium-like cells in the middle of the abscission layer are ruptured. The separation occurs first at the base of the perianth and continues downward until the whole top of the ovary, bearing perianth and stamens, and clasping the style within, curls together and drops off the flower on the second or third day after its opening. The surface left at the top of the ovary after the shedding of the perianth shows clearly that the break takes place in one of the thin cells in the middle of the abscission layer, and also that it occurs in the radial wall rather than as a split between two tangential walls (fig.

62). Whether or not there is a preliminary softening of the cell-walls of the abscission layer, there is evidently a change in the cell-walls of the vascular bundles in the line of fission, as these become flabby and distorted before abscission occurs (fig. 68). Mucilage cells lying in the line of fission are usually not traversed by it, but cells within or without these become transformed into abscission cells (figs. 61, 68).

The lining of the funnel left at the top of the ovary after abscission is thus made up, from the outer edge of the funnel down nearly to its bottom, of the thin-walled cells derived from the abscission layer. Immediately after abscission the outermost cells dry and shrivel (fig. 62), while cells just below the surface begin the production of the protective layer of cork cells which will be noted in describing the fruit (fig. 63). The very bottom of the funnel left after abscission is in most cases formed by the short stump of the style, which is apparently cut off by an irregular transverse rupture of the cells without the formation of any distinct abscission layer. The wall of the funnel for a millimeter just above the stump of the style is still lined by the epidermis (fig. 24). Only in those cases where the abscission layer cuts across below the base of the style (fig. 61) is the corky lining of the funnel complete from the start.

MORPHOLOGY OF THE OVARY.

The flower of this species of *Opuntia,* like that of any angiosperm, is to be regarded as a branch of the shoot which bears carpels, stamens, petals, etc., instead of the usual photosynthetic leaves, but it is unusual, or indeed almost unique, in retaining a large series of the characteristics of the vegetative shoot. This is indicated clearly by certain features of its earlier development, by the occurrence on it of photosynthetic leaves with axillary buds, and by the occasional presence on it of spines, like those of the vegetative shoot. Further evidence tending in the same direction is offered by the persistence and secondary growth of the fruit, by the vegetative multiplication of the flower and fruit, and, finally, by the occurrence of many types of structures intermediate between the typical fruit and the typical vegetative joint. In this assemblage of peculiarities the flowers of this and certain allied opuntias are unique, so far as I can learn from published records. In the allied genus *Peireskia* the primary flower does, it is true, bear several pairs of green leaves, with buds in their axils, and 2 or 3 of these may give rise to secondary flowers. Tertiary flowers, however, are more rare, as far as I have learned, and clusters of more than 3 or 4 mature fruits have not been seen. No record has been found of these axillary buds of the ovary giving rise (either before or after the separation of the fruits from the plant) to vegetative shoots of the sort formed by fruits of *Opuntia fulgida.* In the genus *Cereus* also something of the same kind evidently occurs at times. Thus Harris (1905, p. 535) describes briefly the occurrence, in a specimen of *Cereus boxaniensis,* of " several terminal fruits, one of which had other flowers developing from the side." A section of one of the (primary?)

fruits showed it to be sterile. No information is given concerning the presence of axillary buds on the primary fruit, though it is clear that these must have been present to initiate the secondary flowers.

The nearest approach to this structure of the wall of the ovary in these Cactaceæ of which I find record in any other family is seen in the genus *Calycanthus*. In this form the greatly developed floral axis is depressed at the top to form a cup, from around the edges of which arise the perianth members and the stamens. The numerous distinct carpels, on the contrary, are developed from the bottom of this cup and remain surrounded by it, but do not play any part in roofing it over, as the carpels of the *Opuntia* flower close above its concave growing-point. The outer wall of the cup of this fruit of *Calycanthus* bears the scars of many fallen petaloid floral leaves, distributed much as the leaf-scars and areoles are over the fruit of *Opuntia fulgida*. A study of the development of the flower of *Calycanthus* shows, however, that there are no axillary buds above its leaves. There is not even the smallest recognizable rudiment of this, and hence no possibility of the development of secondary flowers or shoots from the wall of the flower or fruit.

The facts of development and structure suggested in the paragraph before the last, together with those detailed earlier in this paper, furnish important if not conclusive evidence regarding the morphological nature of the ovary of this opuntia. To the writer these facts seem to offer very strong evidence for the view that the flower of the opuntias consists of a shorter or longer vegetative joint, into the depressed upper end of which the ovary is completely submerged, and around the margin of which the stamens and perianth members are inserted. This view has been advanced in more or less definite form by various workers on the Cactaceæ in the past. (See Schumann, 1894, p. 168; Zuccarini, 1844; Toumey, 1905, p. 235; Harris, 1905, etc.) The evidence for this view, however, has hitherto always seemed somewhat inadequate. Since it is felt that the present study offers the most complete chain of evidence thus far produced, especially from the developmental standpoint, this evidence will be stated here in some detail.

In the first place the external structure of the ovary at the time of opening of the flower is very like that of a vegetative joint, having prominent mammillæ, each of them bearing a conical leaf and a bud in the axil of the latter, and (rather rarely) a spine like those of the stem itself. As stated above, the ovaries, and the fruits formed from them, differ markedly in length and breadth. Thus, the basal part of the ovary may sometimes be short, with relatively few mammillæ and areolæ, and so give rise to a nearly globular fruit in which the ovarian cavity reaches nearly to the base (figs. 11, 24, 26, 27). In other cases the basal portion of the ovary may be far more developed, with 20 or even 30 tubercles, and the ovarian cavity may occupy only the upper third or fifth, or even less, of the portion of the whole floral joint below the perianth (figs. 7*b*, 28). In these extremely long flowers the

surface of the ovary at the base may be much more stem-like than at its upper end, having more prominent tubercles and furnished with areolæ that not infrequently bear a spine or two each. Not only do the real functional flowers and fruits differ considerably in size and in the relative development of parts, but the semblance to the stem may go so far that the perianth fails to open, or even fails to develop completely, or (in extreme cases) the carpels or ovules or even the ovarian cavity itself may never be initiated at all.

Perhaps the small, smooth jointlets or pseudo-fruits mentioned by Toumey (1905, p. 531) are to be regarded as the final members of this series of simplified fruits. These pseudo-fruits occur in more or less dense, fruit-like clusters, which Toumey says are particularly abundant in adverse seasons, when true fruits are less abundant. Such structures resemble true fruits in the lack of spines and in the less marked tubercles, but differ in having no trace of a flower or a perianth scar at the terminal end.

These joints (intermediate in character between flowers or fruits and normal vegetative joints) occur still more frequently in the allied species *Opuntia leptocaulis,* in which practically all degrees of reduction of the floral parts can readily be found. Perhaps as complete a series could be found for *O. fulgida* after long search, but the intermediate types are far more abundant in *O. leptocaulis* (figs. 89, 96). In the platopuntias also joint-fruits quite similar in character to those of *O. fulgida* are not really infrequent where large numbers of these plants can be examined in the field. The stem-like character of these joint-fruits is still more clearly indicated in these forms, because the normal joints are flat, while the fruits are usually barrel-shaped or obconcial. A number of examples of these unusual fruits of the flat opuntias have been mentioned in the literature, chiefly on plants growing in greenhouses. Most of these abnormal structures have rather typical perianths, sporophylls, ovarian cavities, etc., but the wall of the ovary, instead of being as usual a radially symmetrical structure, grows out on two sides to wing-like expansions. This gives the whole structure the appearance of a disk-like vegetative joint with a thicker ovary embedded in its upper margin. This ovary may be at the very top or down more or less on the lateral margin of the disk.

Secondly, the internal structure also of the ovary of *Opuntia fulgida* is essentially like that of the vegetative joint. Thus the organization of the areole, the photosynthetic system, and the vascular-bundle system are alike in the two structures, except for the additional vascular branches supplying the perianth and sporophylls of the flower (fig. 28).

A third feature in which the fruit of *Opuntia fulgida* resembles the vegetative shoots of the same plant is in its ability to persist for some years on the parent plant and to continue to grow in thickness year after year by a well-defined cambium layer. This point is dealt with in more detail elsewhere (see p. 29).

Fourthly, the capacity mentioned elsewhere for self-propagation by the attached flower and that of shoot-production by the fallen fruit are still

other features in which these structures resemble the vegetative joints of the shoot.

Fifthly and lastly, the whole history of development of the flower and fruit, when compared with that of the vegetative shoot, shows clearly that the whole lower portion of the ovary, up to the perianth, is developed by a convex growing-point, in every respect just as a branch of the stem is. It is evident that if the growing-point of a flower, when once initiated, continues its activity but a short time before the members of the perianth are laid down, the ovary of that flower will have only a short vegetative portion, and the ovarian cavity will occupy a considerable portion of the whole length of the ovary (figs. 23, 25). If, on the contrary, the growing-point that is to form a flower continues longer to form leaves, areoles, tubercles, etc., there may be a long stretch of vegetative axis developed before the perianth and sporophylls are initiated. Thus the ovary proper may occupy but a small portion of the upper end of the whole segment or joint which is the product of the continuous activity of this individual growing-point (figs. 7*b*, 7*c*, 28).

The comparison of figures 17, 19, 22, and 23 shows clearly that the ovary of this cactus is really secondarily submerged by the upward and inward growth of the portions of the axis just below the perianth. The result of this growth is that the ovarian cavity, at first formed on a level with the uppermost areoles (figs. 16, 17), is buried more and more deeply by this growing upward and rolling inward of the parts of the wall of the ovary that were laid down before the cavity of the ovary had appeared. This differential growth, which, during the ontogeny of the organ, buries the originally nearly superficial and terminal ovarian cavity, until it lies near the middle in the older flower and fruit, suggests clearly the probable phylogenetic origin of the type of fruit found in this opuntia.

A very striking feature of shoot development in these opuntias is the marked constriction usually formed at the limits marking the growths of the same growing-point in successive seasons. This corresponds, of course, to the boundaries marked by the winter bud-scale scars on the shoots of woody dicotyledons. The anatomical reasons for this constriction in these opuntias are not entirely clear. Apparently the protective structures formed about the terminal bud of the annual shoot at the end of the growing-season render the tissue here firm and incapable of swelling out in the following spring to the thickness of the middle portion of this shoot.

The characteristic origin of the flower in the cylindropuntias is also, as we have seen, from a new axillary bud which develops a flower with its longer or shorter ovary in the same season that it pushes out of the areole. In certain rare instances in *Opuntia fulgida, O. spinosior,* and in others seen in *O. cylindrica,* growing at Del Monte, California, the part of a flower-forming joint, containing the ovarian cavity, was marked off from the basal portion only by a very slight narrowing of the joint. Such structures seem to indicate that the same growing-point may sometimes develop continuously either

during the same season, or more probably for two successive seasons, forming a vegetative axis in the first and a flower and fruit in the second. This at least is the most plausible explanation that suggests itself of the origin of such structures as those shown in figures 7*c* and 8S, where nothing but a very slight constriction separates a well-developed fruit from a vegetative joint of the usual length of a year's shoot.

This same sort of change in the nature of the product of a growing-point, either between the beginning and end of the same growing-season or in successive seasons, will probably prove to be the explanation of the origin of certain combination joint-fruits found in the flat-jointed opuntias.

The most interesting problem concerning the development of joint and fruit in these cacti is, of course, that of the cause determining that, up to a certain stage in the history of the growing-point of each flower-rudiment, there shall be formed photosynthetic leaves, tubercles, and areoles only, while beyond this point the course of development is so changed that thereafter nothing but floral structures are laid down about the margin of this identical group of initials. The fact that this change in the character of the rudiments produced on the growing-point occurs at different times in different flowers of the same plant seems to indicate that the conditions controlling this are somewhat local in nature. Such experimental attempts as were made to change the fate of the structures organized about the growing-points of very young flowers, by removing the persistent fruits bearing these young flower-buds, gave no clue to the cause or nature of the change in character of these rudiments. These experiments did, however, show that when the change has once occurred the character and fate of these buds of the areoles are not reversible. In other words, if a fruit of *Opuntia fulgida* is plucked in February or March and placed in moist sand, certain of its areoles will give rise to vegetative shoots. If, on the contrary, the fruits were picked and planted in April, after the floral structures have been initiated, these same areoles wither without giving rise to any permanent structures (*i. e.*, shoot-buds) such as would have been formed by these very same areoles if picked a few weeks earlier. Further experiments are being undertaken in the hope of discovering the material or responsive basis of this change.

It would seem, then, that we have strong evidence, from its structure and development, for believing that the present type of fruit in *Opuntia* has arisen from an originally superior ovary which has progressively sunken more and more into the upper end of the joint bearing it. However, as Harris (1905) has pointed out, there is as yet no adequate evidence for concluding with Toumey (1905) that this submergence has occurred very recently in the phylogeny of the genus or family. It is still possible, of course, that *Opuntia* is a less-modified type of a series of which *Cereus, Echinocereus,* and *Echinocactus* are more highly evolved members. In the latter genera the wall of the ovary may bear numerous bract-like leaves resembling those of the opuntias and often also bear axillary areoles, having more or less abundant trichomes and in some cases one or several spines.

THE FRUIT: ITS STRUCTURE, PERSISTENCE, AND FATE, NORMAL AND ABNORMAL.

The fruit of *Opuntia fulgida* occurs, as we have seen, in clusters of from a dozen to a hundred or more depending from one vegetative joint or even from a single parent fruit (figs. 2, 3). The individual fruit may be globular in form, or barrel-shaped, pear-shaped, or still more elongated and nearly cylindrical (figs. 3, 4, 7, 26, 28). It may have a diameter of from 20 to 35 mm. and a length of from 25 to 65 mm. Its size differs with the plant and with its position in the cluster. The terminal and younger fruits are usually smaller, but sometimes those of any one growing-season seem small throughout. The surface of the upper or terminal end of the fruit is formed by the cork-covered scar left by the fall of the perianth and stamens. This scar is decidedly concave when young, but with age it flattens out or, in some cases, even bulges slightly at the center (figs. 3, 25, 28). The lateral surface of the fruit when young has markedly developed tubercles, or mammillæ, each terminating in a leaf-scar and its accompanying areole (figs. 4, 17, 31, 32, 47). These tubercles become less prominent as the fruit grows older and at last nearly disappear, though traces of them are seen in the pentagonal or hexagonal form, in cross-section, of older fruits (figs. 3, 26, 43).

The internal structure of the fruit is far more variable than that of the exterior. It may have no seeds at all or it may contain anywhere from 1 to 200 or more seeds. These seeds may all be shriveled, partially developed rudiments, or from a few to most of them may possess normally matured embryos. The number, condition, and structure of the seeds seem to show no correlation with the external form of the fruit (figs. 25, 26, 28).

The most striking peculiarities of the fruit of this *Opuntia* are, as suggested above, its failure to ripen, its persistence on the plant, its long-continued growth, and finally its capacity for proliferation, whether left attached to the parent plant or torn loose from it.

THE FRUIT AT THE TIME OF ABSCISSION OF THE PERIANTH.

With the dropping from the ovary of the stamens and perianth we have left the earliest stage of the fruit proper. Externally, the fruit so formed is a globular or obconical structure, with a very deep, funnel-like depression in the top and from 15 to 40 strongly raised tubercles on its sides. Each of the latter bears a leaf-scar and a more or less developed areole at its upper end, which was mentioned in describing the ovary of the flowers.

In internal structure this young fruit consists of the superficial epidermis, which is soon continued over the leaf-scars and perianth-scars by a corky periderm. Below the epidermis is the 4 or 5 layered hypodermis, consisting of an outer layer of crystal-holding cells, and within this of 3 or 4 layers of collenchymatously thickened cells, in which the cell-cavity is finally to be nearly obliterated (figs. 71, 72). Within the hypodermis are the elabor-

ately ventilated, photosynthetic palisade of the cortex, with its scattered slime-cells and crystal cells, and the complexly reticulated vascular system; and, finally, within the latter and between its meshes are many layers of mucilaginous storage parenchyma. The latter in turn surrounds the cavity of the ovary, now nearly filled by the young seeds and by the mass of loose tissue arising from their long, coiled, funicular strands (figs. 23, 40, 71).

The somewhat uneven outer layer of the epidermis of the projecting tubercles consists at this stage of rather cuboidal cells, with bulging and considerably thickened outer walls (fig. 71). The epidermal cells of the grooves between the tubercles are somewhat elongated radially and thinner-walled than those of the outer margins of the tubercles just described. Stomata are scattered rather frequently over the surface of the tubercles. The guard-cells are already sunken considerably below the surface, though not as far as in the mature fruit (figs. 71, 72). The inner layer of the epidermis already includes many crystal-containing cells of the sort figured in detail in the older fruit (fig. 71, 72, 73).

The cork of the fruit at this stage is confined to the pit-like scar at the top of the fruit, where it forms an ashy-white layer. It consists, outside the phellogen, of above 8 to 10 layers of rectangular cells approximately 100 microns long and broad and 20 to 40 microns thick, radially. The walls of all save one layer of these are not greatly thickened, nor apparently strongly suberized (fig. 63). The very bottom of this cup around the stump of the style is commonly still protected only by the original epidermis, which, as was noted earlier, is often not cast off along with that part of the lining of the cup which bears the stamens (figs. 23, 60).

The photosynthetic tissue of the ovary-wall has already begun to assume the striking arrangement in radial rows that is so characteristic of the cortical tissue of the mature fruit as well as of the vegetative joint (figs. 39, 70, 71, 73). Scattered abundantly through this palisade, which extends inward 8 or 10 cells from the surface, are numerous mucilage-cells of the usual more rounded form.

The vascular-bundle system of the young fruit consists of about 16 primary bundles entering it at the base. These soon divide by dichotomous forking to form twice as many bundles at the level of the lower end of the ovarian cavity. The repetition of this forking gives rise in the upper half of the fruit to a still more complex system of main vascular bundles (figs. 17, 21, 25, 26). From the points of forking of these main bundles are given off the groups of smaller bundles, one group at the base of each tubercle, to supply the tubercle, its growing-point, and the leaf and nectaries arising from it (figs. 21, 27, 28, 32). The main vascular bundles are nearly isodiametric in cross-section at this stage of development, and are about 500 microns thick radially and 300 microns broad tangentially (fig. 44*a*). In internal structure, which may be noted briefly for comparison with the bundle of the older fruit, each main bundle includes about 25 or 30 tangen-

tial layers of xylem elements. Outside of these lies a group of 6 or 8 layers of radially arranged cambium-cells and their little modified derivatives. Still further outward on the same radius is the half-cylindrical strand of phloem-cells, about 15 to 20 cells thick radially (fig. 44*a*). From a ring of anastomosed bundles near the rim of the funnel at the top of the fruit a series of downward-growing branches gives rise to the 6 or 7 pairs of placental bundles, one pair running longitudinally behind each double row of ovules (figs. 11, 22, 23, 26, 28, 38, 39, 41). From this same vascular ring numerous small branches grow inward and upward. These are the ones that supplied the stamens and perianth members before they were shed. Other similar branches grow still farther downward and then turn upward to form the 6 or 7 bundles of the style and stigmas (figs. 20, 22, 23, 28, 37, 41, 61).

The most important structures within the fruit—the seeds—arise, as we have seen, in a double row on each of the 6 or 7 placentæ. There are from 8 to 12 or more young seeds in each row, making from 100 to sometimes 200 or more seeds that are initiated in the fruit as a whole. Usually not all of these mature. Sometimes, as noted above, none of them mature. At the time the perianth is dropped there is a decided difference in size among the seeds present in any one ovary. The most developed are about 0.5 mm. in diameter inside the pocket of the funiculus in which each seed is inclosed and about 0.25 mm. thick. The seed-coats are unthickened and have only 2 layers of cells each. The embryo sac has usually reached the 8-nucleate stage. The cavity of the ovary is at this time about half filled with the seeds and the swollen funiculi or seed-stalks.

THE MATURE FRUIT.

At the end of the growing-season, which in Tucson terminates about the middle of October, the fruit has attained what must be regarded as a mature stage. The seeds within it are now full grown. These mature fruits, of from 3 to 5 months' growth, differ considerably in shape and size. They are commonly pear-shaped, or somewhat more rounded, and have a diameter of 12 to 15 mm., with a length of 20 to 35 mm. or more (figs. 3, 7, 8). Later fruits of the season may be as large as, or even larger than, the earlier ones. Fruits of one season may average in all dimensions larger than those of the season before.

The surface of the typical fruit at maturity has filled out so that the tubercles have lost their prominence. The areoles differ in size on the same fruit, the upper or larger ones at this time being 15 to 30 or even 35 mm. in diameter. Occasionally an elongated fruit will be formed which has much the appearance of a mammillate vegetative joint, except for the presence of the perianth-scar at the top and the fact that the spines are weaker than in most joints (fig. 7).

The most important features of the internal structure of the fruit are those concerned with the vascular bundles of the wall of the ovary and with the

character and contents of the ovarian cavity. The main vascular bundles of the wall increase only moderately after the fall of the perianth, though they do increase somewhat in radial dimensions by the addition of new layers of xylem tissues (fig. 44*b*). The amount of the cortical parenchyma outside the vascular bundles may also increase somewhat, and this latter growth is probably the cause of the rounding out of the fruit and the disappearance of the mammillæ (figs. 3, 7*b*, 8).

The number and character of the seeds present in different fruits differ markedly. There may sometimes be an ovarian cavity filling three-fifths of the diameter of the fruit, or this cavity may be practically wanting. About half the mature fruits contain one or more ripe seeds, which vary in number from 1 to 100 or 200 per fruit. The other half of the fruits have only small ovarian cavities in which the seed rudiments have ceased their development at different stages from half-formed ovules up to half-grown seeds (fig. 23). In some cases not even these withered rudiments can be found in the place where the ovarian cavity should be.

A consideration of the facts related inclines at first to the conclusion that ovaries mature into fruits only when pollination has occurred and that seeds form only when the further process of fertilization has taken place. This seems doubtful, however, in view of the fact that many seeds may go halfway through their development before degeneration sets in. The attempt is being made to determine the distribution of these different types of degeneration in different plants and different flowers of the same plant.

The most striking peculiarity of these mature fruits is that they do not ripen. From analogy with all other fruits, we should expect at this time that the flesh of the *Opuntia* fruit would either change color and soften or harden up to form a dry fruit. But nothing of this sort happens. The matured fruit, with its color still bright green, with its photosynthetic tissues still active in starch-making, and its well-established fascicular cambium simply halted until the next spring, enters into the resting-period of 4 or 5 months. There is not the slightest sign of ripening or any change at all comparable with this process. There is no preparation of any sort for the discharge or escape of the seeds to conditions conducive to germination. On the contrary, the majority of the mature fruits normally remain attached to the parent shoot, not merely through the succeeding fall and winter, but season after season for several or many years. These persistent fruits become essentially a part of the vegetative shoot, performing not only the photosynthetic function of a vegetative joint, but also budding out new shoots. Usually these shoots arising from attached fruits are floral shoots. More rarely a vegetative joint may arise from such a fruit, and then the latter becomes a constitutent joint of the vegetative branch, undistinguishable except by its perianth-scar and usually by its lack of spines (fig. 79). The fate of a fruit in these respects is the same, whether it contains many fertile seeds or whether, as may often be the case, it is entirely seedless.

THE PERENNATING FRUIT: ITS STRUCTURE AND SECONDARY GROWTH.

The matured fruits of *Opuntia fulgida* not only do not ripen at the end of the growing-season, but (as noted above) they are neither shed from the plants as most fruits are, nor do they open in any way to discharge their seeds. On the contrary, these fruits remain year after year, attached and actively growing, until they may become 40 or 50 mm. in diameter and 70 or 80 mm. long. The growth of these fruits in length must be chiefly primary; that is, each fruit attains practically its maximum length during its first season's growth. Thus the longer fruits mentioned must have been exceptionally long at the start.

Growth in thickness of the larger fruits is, on the contrary, largely secondary. It is accomplished by the persistent activity of the fascicular cambium and by the general multiplication of the parenchyma cells between the bundles. Whether there is an increase in the central medullary parenchyma of the fruit has not been determined with certainty, but there appears to be some little increase in the interior diameter of the vascular ring. The cortical parenchyma, inside the hypoderm, may increase in thickness from about 2 mm. in the just-matured fruit to 5 mm. or more in a fruit several years of age. This radial growth seems to be almost entirely a result of the radial elongation of the cortical cells, as the number of these along a radius ranges from 20 to 25 in both the just-matured fruit and in that 3 or 4 years old.

The fascicular cambium of the perennating fruit gives rise to numerous phloem and xylem elements, which increase the radial dimension of the bundle from 0.7 or 0.8 mm. in the newly matured fruit to 3 or 3.5 mm. in a fruit several years old. The radial extent of the xylem in the newly formed fruit is about 0.6 mm. and that of the phloem 0.2 mm., while in an older fruit the dimensions are 2.6 mm. for the xylem and 0.6 mm. for the phloem. This shows that the growth of the two tissues has kept their bulk much the same relatively. The tangential growth of the bundles is relatively slight, the outer edge of a bundle 4 or 5 years old being only half as wide again as that of one in the first-year fruit. No definite annual rings could be distinguished in the wood of these older fruits. The number of larger xylem elements along a single radius in a young fruit is about 25, while in a 4 or 5 year fruit there may be 80 or 90 vessels on a single radius.

The parenchyma of the pith-rays differs from that of the cortex by showing a vigorous cell multiplication. The pith-ray of the just-matured fruit may have but 8 or 10 cells in the radial extent of the bundle, while in a fruit 4 or 5 years old a pith-ray may be made up of 25 or 30 cells in the radial width of the bundle. This growth is apparently due to the general division of cells throughout the ray, as no trace of an interfascicular cambium is discoverable.

Two structures only on the surface of the fruit undergo important changes as the fruit ages. These are the corky periderm and the areoles. At the

end of the season of its origin the fruit is protected by the well-cutinized epidermis and the underlying hypodermis, except for the perianth-scar and the individual leaf-scars. This epidermis persists over the general surface of the fruit for several years. Only where the epidermis is cracked by the swelling of the fruit or is otherwise injured is the original protective layer replaced in function by cork, like that of the perianth-scar.

The periderm of the perianth-scar has its origin, as we have noted, from a phellogen layer arising in descendants of the original cells of the abscission layer, just within the plane of abscission (figs. 62, 63). The first 5 or 6 layers of cork cells formed by the cork cambium are very thin-walled; then there is formed a single layer of very thick cells (see Wolfe, 1912, figs. 6, 7, 9). These sclerenchyma-like cells have walls of a pale-yellow color, which in older fruits are made up of from 15 to 20 distinct layers marked by numerous minute radial pits (figs. 63, 64, 65). The walls stain intensely with safranin and gentian violet. The cork cambium, after forming this thick layer, may continue to form more thin-walled cork cells until, in the older fruits, 12 to 15 or more layers are present inside the intact, thick layer. These later layers are more numerous on the upper margin of the perianth scar. With increasing age the 5 or 6 layers of thin cork outside the sclerenchyma layer, which are left more or less shriveled after abscission, are gradually worn off from the more exposed parts of the scar. This leaves the sclerenchyma as the superficial and essentially protective layer unless this is injured. When this primary sclerenchyma layer is broken a secondary one is formed immediately outside the then active phellogen (fig. 14, at right).

Periderm formation in the region of the areole begins soon after the fall of the leaf, in an area that includes tissue of the leaf-scar itself and a few of the epidermal cells below and beside this (fig. 14). There is thus formed a periderm of from 3 or 4 to 8 or 10 cells in thickness, of which the portion immediately above the foliar bundle may finally include 3 or even 4 immediately superposed sclerenchyma layers (figs. 63, 64). As development of the areole proceeds the cork layer develops upward from the leaf-scar and thin-walled cork-like but apparently little-suberized cells are formed immediately beneath the persistent trichomes, just above the leaf. Later the formation of these cells continues on beneath the bases of the withered nectaries and spines if there are any, and finally beneath the bristles (figs. 14, 17). The latter, in older fruits, may be supported upon 12 to 15 or more layers of clear thin-walled cork-like cells (fig. 14). The only parts of the areoles that are not covered are the growing-point and the immediately surrounding series of rudiments of nectaries, bristles, etc. These all lie well-protected at the base of the dense tuft of younger trichomes that overhang the growing-point (fig. 50).

On the lateral surface of the older fruit corky tissue may arise by the extension of the cork about the areole, or that of the perianth-scar over the edge of the cup, or it may arise *de novo* from injured spots in the clear epi-

dermis between the areoles. In this way considerable portions of the surface of a fruit 4 or 5 years old may become covered with cork developed below cracks or bruised spots, and the fruit thus come to have the mottled green and gray color characteristic of maturing vegetative joints (fig. 3). The effect of this cork, aside from affording protection to the water-stored cortical tissues, must be also to cut off the light and air from the photosynthetic cells of the portion of the fruit covered by it. While lessening its starch-making capacity, the cork is thus of prime importance to the fruit in maintaining it as a supporting and conducting structure for the flowers and persistent fruits that may arise from it year after year.

The structure of the areole in the young fruit has already been discussed (p. 12). The chief change in the areole with increased age of the fruit is the increase in size, until it may become 3 or 4 mm. broad and 6 or 8 mm. long in the case of those near the top of the fruit. This increase in size is due chiefly to the continued production of hundreds of trichomes year after year. These appear in rather definite concentric circles around the growing-point. Besides the trichomes, the areole also forms additional nectaries, year after year, till at least a score may successively develop and wither. The bristles of the fertile areole, as has been noted, are not increased in number after a flower is initiated (figs. 14, 17, 50). The sort of development here indicated is the characteristic one for many of the areoles of the upper half of the ovary throughout the life of the fruit. Others of the basal half or quarter of the fruit may persist, but show only slight growth for 2 or 3 years and then cease growing altogether.

Other of the upper areoles, several in each fruit, give rise to one or the other of the two most important structures developed from fruits. These are the floral shoots that may arise on the attached fruit and the vegetative shoot that develops from the areole of a detached fruit. These structures are, of course, the normal products of axillary buds. Hence the earlier period, during which these areoles are developing only modified structures like bristles and nectaries, must be regarded as a sort of resting-period in which the normal activity of the bud is inhibited.

When the normal development of an areole is accomplished and a shoot produced, all further activity by this areole is terminated, as must be evident from the fact that the whole mass of the single growing-point of the areole is embodied in either the vegetative shoot or the flower. The exact conditions conducive to the production of a flower in one case and a vegetative shoot in another, with the details of development of each, will be described, as far as known, in the discussion of proliferation (see pp. 35-50).

The possible activities of the fruit of *Opuntia fulgida* may be summarized as follows: The fruit usually remains attached and in succeeding seasons buds out new flowers. If fruits fall to the ground from increasing weight of the cluster or when dislodged by wind or browsing animals, then any one of three things may happen. Most frequently the fruit dries up or decays

and nothing comes of it. If it drops on moderately moist soil, then it may give rise to roots and shoots by proliferation from the areoles. More rarely still, the fruit may set the seeds free by decay and the latter may possibly then germinate to seedling plants. This latter fate, which must be regarded as the most normal one for such a fruit, is evidently a very rare one for the fruit of *Opuntia fulgida,* at least in the deserts near Tucson, where seedlings have never been seen.

THE SEED: ITS STRUCTURE, PERSISTENCE, AND GERMINATION.

The ripe seed is the one essential structure of the fruit which remains entirely unchanged year after year, as the fruit persists on the parent plant.

The mature or ripe seed is an irregular, round-angled, flattened disk about 5 mm. in diameter and 1.5 to 2 mm. thick in the middle (fig. 77). It usually bulges on both sides of the disk, but often far more on one side than the other. The majority of good seeds are pale yellow in color, with remnants of many colorless cells from the fleshy ovule-stalks sticking to them. In internal structure the seed consists of a well-developed curved embryo bent in the plane of the disk-like seed, of a small remnant of endosperm near the center of the seed and embraced by the bent embryo, and finally of a protecting jacket, formed chiefly by the layers of tissue arising from the pocket of the funiculus, but including also the two thin integuments (figs. 76, 77).

The embryo is from 0.7 to 1 mm. in diameter and about 4 or 5 mm. long. It is bent in the plane perpendicular to that of the adjacent faces of the cotyledons. Most of the cells of both cotyledons and radicle of the embryo are densely stored with what appear to be aleurone grains and slime globules. These bodies take on a brownish and not a bluish color with iodine, and show structural features not characteristic of starch-grains. Occasional cells of the cotyledons and upper part of the radicle are completely occupied each with a large crystal of calcium oxylate like those found in the parenchyma of the mature plant.

The endosperm, which consists of a small mass in the bend between radicle and cotyledons and of thinner layers extending along beside the radicle and over the tips of the cotyledons (fig. 98), is densely stored with starch which reacts in the usual way with iodine.

Small fragments of perisperm, left in the corners where the embryo fits the integument less accurately, are filled with granules reacting like those in the embryo itself. The cell-contents of both embryo and endosperm seem to remain entirely unchanged in fruits that have persisted on the plant for many years after the maturing of the seeds. The integuments are made up of considerably thickened cells, the outermost layer of them with wavy brown walls.

The jacket derived from the funiculus surrounds the seed completely, having finally closed in above the micropyle (fig. 97). It makes up more

than nine-tenths of the thickness of the coat surrounding the seed and consists of three distinct layers. The inner layer is from 150 to 300 microns thick. It consists of intertwisted threads or fibers which run meridionally about the seed. The component cells of these threads are 8 to 10 microns in diameter each by 150 or 200 microns long. The middle layer of the funicular pocket is made up of somewhat similar interwoven threads running equatorially, *i. e.,* around the margin of the disk-like seed. The cells of this layer are 20 to 25 microns in diameter, but only 50 to 60 microns long. The third or outermost layer of the seed-coat is very uneven, consisting of a single layer of cuboidal cells 30 or 40 microns thick, about most of the margin of the seed, but of 7 or 8 layers with a total thickness of 400 microns on the sides of the seed. It is this greater thickness of the outer funicular layer that makes up most of the bulge on the flat side of the disk-like seed.

The whole structure and condition of the seed apparently remain quite unchanged year after year so long as the fruit containing it remains attached to the tree. Not only are the embryos of seeds from the oldest attached fruits still plump, with the stored starch intact, but a seed from such an old fruit is just as capable of germinating as one from a fruit just matured.

A very important question arising in this connection is: Why do not these seeds, immersed in the moist pulp of the parent fruit and raised each summer to a relatively high temperature, germinate there, without waiting to escape from the fruit? The attempt was made to germinate seeds under these conditions by treating them in the manner which was found necessary to secure germination outside the fruit, that is, by chipping the seed-coat. Seeds with the coats cut off at one edge were carefully inserted in the pulp of sound fruits with every precaution not to injure the fruit more than necessary. The wound was then sealed with vaseline and set in a moderately moist chamber to induce germination. No germinations of seeds under these conditions were secured. In each case, whether the injured fruit dried out, decayed, or took root in the soil, the embryo of the inserted seed after some weeks blackened and died. The explanation of this failure of the seed to germinate in its own fruit or in the host fruit was not discovered. It is, of course, possible that it may be found in the mere exclusion of oxygen by the seed-coat or by the mucilaginous pulp of its own or the host fruit. On the other hand, it is quite possible that the osmotic or chemical character of the cell-sap of the pulp surrounding the seeds is the real obstacle to germination.

During two sojourns at Tucson the attempt was made to test the common report that seedlings of *Opuntia fulgida* do not occur in the field about Tucson (Toumey, 1905, p. 360). Diligent search was made for them in many groves of these trees in the months of April and May of 1912 and 1915, but not a single undoubted seedling of this species was discovered. Examination of large numbers of fallen fruits showed no sign of germination of the seeds. It then occurred to the writer that a search on a cattle

range outside the protected, ungrazed property of the Desert Laboratory might show that seedlings arose from seeds that had passed through the alimentary canals of cattle that had eaten the fruits. This search also proved futile. It is of course possible that seedlings may occur in other parts of the area of distribution of this opuntia, or in the Tucson region itself, at other seasons.

With the hope of discovering something regarding the cause or causes of this failure of the seeds to germinate naturally, the attempt was made to germinate them artificially. In the first place, dozens of plump seeds likely to possess good embryos were repeatedly, in spring, autumn, and winter, sown on soil or on filter-paper, and put either in a warm greenhouse or on a warm bath at 30° to 35°. Not a single germination was obtained from these experiments.

Other series of sowings were made of plump and apparently fertile seeds from which the seed-coat had been cut or filed away at one part of the margin. Out of several dozens of these cut seeds sown between layers of damp filter-paper in a gallon battery-jar, only about 8 or 10 germinated. The best proportion of germinations obtained was 5 embryos out of 25 probably fertile seeds.

The difficulties in determining what proportion of seeds are capable of germination are two. In the first place, it is impossible to tell from its external appearance whether a seed has a normal, well-developed embryo or not. Quite aside from the half-developed and withered seeds, there are many of mature size, and apparently plump and healthy, which upon being cut open reveal no embryo at all, or a discolored and shriveled one with no stored material in it. Secondly, of the seeds that are cut into far enough to determine whether they contain good embryos, or far enough to make certain the escape of the swelling embryo from within, some may be so injured as to prevent germination of any sort.

The trials made thus far show that a certain relatively small percentage of the seeds of this opuntia are fertile and capable (if aided in getting out of the coat) of producing normal seedlings (fig. 76).

PROLIFERATION OF FLOWERS AND FRUITS.

The most unique peculiarity of the flower or fruit of *Opuntia fulgida* is its ability to produce new shoots. These shoots may be floral shoots only, as in the case of the attached flower or fruit, or they may be vegetative shoots, as in the case of detached fruit. This capacity for proliferation is dependent, as has been noted, on the presence and persistence of the axillary buds or areoles of the wall of the ovary. These axillary buds are unknown, as far as the writer has been able to learn, on the ovary of any other family of plants, and even in the Cactaceæ occur only in the genera *Opuntia, Nopalea,* and *Peireskia.*

The structure of these areoles, with a description of the rudiments present in them, has already been noted (p. 11). We have seen also that most of the areoles of a flower and fruit may persist year after year without developing anything but minor organs, such as nectaries, trichomes, and spicules. We have now to consider the very important function performed by certain of the areoles in their proliferation to shoots of limited or unlimited growth. There are three types of proliferation by the areoles of the ovary of this opuntia. In the first place, from 1 to 5 or more of the areoles of the unopened flower may give rise to the buds of secondary flowers, which open soon after the primary ones. Secondly, one or several areoles of an attached fruit may in the first or in some later season after its development give rise to primary flowers of that season. Thirdly, the areoles of a detached fruit that has been separated from the parent plant after maturing and placed on moist soil may give rise, first to adventitious roots and then later to the characteristic joints of vegetative shoots. The fruit thus performs the unique function of initiating a new plant by purely vegetative propagation.

PROLIFERATION FROM ATTACHED FLOWER BUDS.

The primary flowers of the season arise in either April or May on either the vegetative joints or the fruits of the preceding season or sometimes on those of a still earlier season. These flowers are developed from the growing-points of the upper areoles of the joint or fruit (fig. 47) in the manner noted above (p. 9).

Before the primary flower is half-grown the buds of secondary flowers of various sizes can be detected developing in from 1 to 4 or 5 of its upper areoles (figs. 9*a*, 9*b*, 13). By the time the primary flower is ready to open, soon after the middle of May at Tucson, the larger buds of the secondary flowers are about one-sixth grown, and are recognizable as buds of flowers rather than of vegetative shoots (figs. 9*a*, 9*b*, 47). About 4 weeks after the primary flower withers and sheds its perianth, the largest secondary flower in its turn opens. This occurs usually between the middle and end of June, and the buds of the tertiary flowers are then already well developed in their

upper areoles. In the latter part of July flowers for the fourth generation of the season are developing from the areoles of the tertiary ones (fig. 6). These quaternary flowers probably open during August, and since the blooming-season may extend into September (Lloyd, Plant World, 1917), it is probable that a fifth generation of flowers may be formed in a single season. No undoubted examples of this, however, have thus far been seen, and I have not been able personally to seek them at Tucson at the proper season.

Since the fruits resulting from the four generations of flowers remain attached to each other in the order of their development, it is clear that a chain of fruits of at least four successive links may be developed in a single season. This has been recorded by Toumey (1898), who apparently believed that all chains of fruits arose in this way in a single season. He definitely mentions that the " proliferous fruit hangs in pendulous clusters, sometimes as many as 7 fruits in a single cluster, one growing from the other in continuous succession." He regards the persistence of fruits over winter and the formation of flowers from them in the succeeding spring as a rare occurrence.

The time of maturing of the seeds of the fruits of the four successive generations may differ considerably, since the fruits continue to grow after dropping the perianth, but even the latest and smallest ones may contain ripe seeds in October. All four links of the chain may commonly persist attached throughout the winter and give rise to new flowers the following spring. Not infrequently, however, the younger, quaternary fruits may wither more or less during the winter and (failing to develop flowers upon them in the succeeding spring) may be crowded off by the new flowers developed beside them on the tertiary fruit by which they themselves are borne.

The formation of these chains of fruits of four links in a single season is thus the result of the continuous uninterrupted development of the growing-points of certain areoles of each successive floral shoot. The structure thus formed is comparable with that developed by many herbaceous plants and the water-shoots of certain woody ones, in which each (or many) of the axillary buds develops continuously during the season of its initiation into a mature vegetative or reproductive shoot.

Other areoles of the flower and fruit of this opuntia have quite an opposite fate. In these the axial bud does not develop continuously, but (after developing a considerable number of trichomes and spicules and a few nectaries) rests till the next growing-season, or sometimes for three or four seasons, before renewing its development.

PROLIFERATION OF PERSISTENT ATTACHED FRUITS.

While certain of the upper areoles of a flower may, as we have seen, develop at once into secondary flowers which open soon after the primary one, other areoles of the same or another flower may practically cease growth with the opening of the flower and persist over one or more winters as resting buds. These buds, retaining their capacity for further development, may give rise, in the succeeding or a later spring, to the primary flowers of that season (fig. 4, 7*c*). Such flowers may arise from any of the 4 or 5 younger fruits of a chain (fig. 4).

The development of these flowers, arising from resting buds of persistent fruits, is identical with that of flowers arising from the areoles of flower-buds, and the fruits formed in the two cases can not be distinguished. The flowers arising from fruits, just as those from the areoles of unopened flowers, may give rise in turn to buds of secondary flowers, and these to tertiary and perhaps quaternary ones in the same season. The repetition of this process of budding out flowers from fruits and then flower from flower several times each season, when repeated season after season, results finally in the formation of fruit clusters of great size. Clusters of 20 to 30 fruits are common, and clusters of 100 or more fruits of all ages suspended from a single parent fruit are not rare (figs. 2, 3). Some of the longer chains may embody 12 or 14 generations of fruits in a single chain (fig. 77). Since, as we have seen, certain of the links added in any one season may wither and fall off, it is evident that a chain of 12 generations of fruits does not represent merely the growth of three seasons, 4 fruits per season, but may represent the product of five or six seasons; in fact, the size and appearance of some of the basal fruits of these clusters indicates an age of more than 6 years. The records of the effect of exceptionally cold winters on the plants at Tucson show that it must often take many seasons to build up a chain of 12 or 14 links. Thus, in the winter of 1912-13 there was an exceptionally hard freeze, soon after which great numbers of the younger persisting fruits fell off the trees, so that chains of more than 3 or 4 links were hard to find. Such a periodic shortening of the chains, even if it occurred but once in three or four winters, would increase considerably the number of summers necessary to produce chains of fruits of the total length of the longer chains found.

The ease with which these fruits may be set free from the plant will be the more readily realized when we note the very slender stalks by which the heavy fruits are attached (figs. 25, 26). These stalks also, especially in the younger fruits, have little lignified tissue. Jarring of the tree by wind or by browsing cattle, which eat many of the fruits in dry seasons, may shake off numbers of fruits that are often found strewn thickly beneath larger plants. The stalks of the older fruits, on the contrary, become steadily thicker and stronger, and the upper ones are thereby enabled to hold the heavy clusters that hang from them.

PROLIFERATION OF FALLEN FRUITS.

If the fruit of *Opuntia fulgida* remains attached to the tree the only structures produced by its areoles are trichomes, nectaries, and flowers. This is practically universally true. Among many hundreds examined, only two cases were seen in which a vegetative shoot had arisen from an attached fruit. If, however, fruits are plucked from the tree and placed on moist soil, there arise from their areoles not flowers but roots and later vegetative shoots, and so new plants are initiated; that is, if any given fruit remains attached there may arise from the growing-point of a certain areole a relatively short shoot which develops leaves and axillary buds, but soon ends its activity with the formation of a set of stamens and carpels. If the same fruit were detached the same areole, and thus the very same growing-point, may give rise to a shoot of unlimited growth, while other areoles near the soil form adventitious roots. This production of new plants from buds on the wall of the ovary in the fruit is a surprising phenomenon; in fact, it is as unique as the formation of flowers from axillary buds of the ovary of the unopened flowers.

This process of the vegetative sprouting of a fruit planted in soil to a new plant often occurs in 50 to 75 per cent of fruits planted in the greenhouse. In the field about Tucson, at least in the spring of the year, it occurs but rarely. A careful examination of some scores of young plants of this species, of 3 or 4 joints in height, in the desert near Tucson, in May 1915, showed that all had arisen from fallen vegetative joints. None of the fallen fruits seen at this time showed any preparation for the development of new plantlets. This is the more surprising because the soil had been considerably moistened that season by unusually copious rains. In September, however, a careful search by an assistant, B. R. Bovee, revealed a few very young plants which had evidently arisen from fallen fruits. It is possible, therefore, that under some conditions, such as those existing during years of favorable summer rains, a considerable number of new plants may thus arise from fruits.

The origin of new plants from rooted fruits will be described as it has been observed in the greenhouse. The process is clearly the same in the field, as far as could be seen from the few plantlets found there. Many different plantings of the fruits were made at Tucson in April and May, at South Harpswell in July and August, and at Baltimore in February, October, and December. These all gave substantially the same results, in spite of the fact that the Tucson plantings were of fruits that would in a week or two have produced flowers if they had been left on the parent plant, while those planted in Baltimore had entered into the resting-stage for the winter (figs. 78, 99).

Fruits that are half-buried in a soil that is kept moist but not saturated may begin to form adventitious roots within the first week. In 5 weeks' time the fruit has been found fastened securely in the soil by several roots, some

of them 5 cm. long, 1 mm. thick, and often branched several times. These roots arise chiefly on the buried portion of the fruits and always develop from an areole, from the broken surface of the fruit-stalk, or more rarely from near the edge of the perianth-scar. From this statement it will be seen that roots may arise at either the basal or apical end of the fruit, or at both, depending on whether the fruit is laid horizontally or whether one end is placed lower in the soil. My observations do not confirm the conclusion of Toumey (1905) that the " roots appear chiefly at the basal end of the fallen joint." Though the roots arise from the areole, they do not arise from its growing-point, in the middle of the areole, but from the still active tissue around its edge. Very often a root pushes out above the cluster of bristles on the adaxial margin of the areole, but a root may rise also from any other part of the margin (fig. 100). One or several roots may arise from the same areole. When a root is developed from the scar of the fruit-stalk it is usually from its margin. As such a root matures, however, the vascular bundles of the root soon come to form continuations of the bundles at the base of the fruit. When a root develops on a perianth-scar it appears always to originate in the region of the cork cambium, and it breaks through the cork itself in emerging (figs. 78, 99, 100).

The initiation of a shoot by a detached fruit does not occur until some time after the first roots are developed on it. The formation and functioning of roots are apparently necessary antecedents to shoot formation. In fruits planted in the greenhouse at Tucson on April 26, kept well watered and at rather high temperatures, shoots began to push out of some areoles by May 25, and on the following September 10 all but one or two of the 18 fruits planted had one or more vegetative joints on it. Some of the latter were 2 cm. long. Similar results, though not so universally successful, were obtained from plantings at South Harpswell and Baltimore. One lot of fruits planted at Baltimore produced shoots only 3 or 4 cm. long in a year; while others, with more soil, had shoots 10 cm. long in five months.

One or several joints may arise from each fruit, either simultaneously or successively. They may arise from areoles on the exposed surface of the planted fruit or sometimes from those joints at the surface of the soil, but nearly always from the larger areoles of the apical half of the fruit. This is without regard to whether the fruit is planted on the side, with apex down, or with the base down.

The shoot arising from the areole of a fallen fruit is formed by the growing-point of the areole, just as a flower is, or just as a branch is from a vegetative joint. The new shoot, however, is for a long time different from the branch of a mature plant in remaining slender and in the permanent delicacy of its spines (fig. 78). In fact, it has the appearance of one of the early joints of a seedling. The primary shoot, as developed in the greenhouse in Baltimore, usually does not branch until the second season. Quite early in its development the new shoots, especially if it has arisen near or under the

soil, sends down adventitious roots of its own which soon become an important part of the root-system of the new plant.

From what has been said of the slow development of plantlets from sprouting fruits in the laboratory, it is evident that it takes a number of years to develop a mature flowering plant from a fruit. It is doubtful whether such a plant can mature more than a year or two sooner than a seedling started at the same time.

Examination of plantlets, from sprouted fruits and also of those from fallen joints, shows that not all of the fallen fruit or joint enters into the make-up of the first or basal joint of the new plant. The portion which does so probably depends in part upon the position in which the fruit falls, or is planted, on the soil and on the relative positions on the fruit of the areoles forming the roots and those forming the shoots. It is a common occurrence for a part (often a fourth or a third) of the fruit, including both cortex and vascular bundles, to be cut off by a layer of cork from the part going into the first joint of the new plant (fig. 99). The phellogen from which this cork arises is formed by the parenchyma of the cortical and medullary tissues.

The fate of the different parts of the vascular system of the parent fruit has not been followed out in all details, but it is clear that much of the old system plays no important part in the new plant and that some of it is cast off with the cut-off portion of the fruit (fig. 99). The chief part of the old system to do service in the new plantlet is that which lies most directly between the point of origin of the adventitious roots and that of the primary shoot of the plantlet (fig. 99). These strands quickly become thickened to many times the diameter of the other bundles of the parent fruit. The seeds present in these sprouting fruits evidently persist indefinitely in the flesh of the latter. Their ultimate fate has not yet been determined, as the oldest plantlets seen which were known to be of this origin were but 2 years old.

While roots may arise from parts of the fallen fruit outside the areole, such as the scar of the fruit-stalk or of the perianth, it is apparently not possible for shoots to arise elsewhere than from the areole. The experiment was tried repeatedly of planting fruits, all the areoles of which had been destroyed by cauterization, to determine whether other superficial tissues might be stimulated to produce new-shoot growing-points. Though some of these cauterized fruits took root in the soil and remained plump and green for 24 months, they developed no visible rudiment of a shoot.

An attempt was made also to determine whether halves or quarters of a fruit, in which the cut surfaces were either covered with vaseline or dried, could be made to take root and form new shoots. This was partially successful in only a few instances where part of the piece remained green for a time and some roots were formed, but in no case was a single shoot formed. This was due apparently to the fact that a softening and decay of the exposed pulp of the cut fruit took place, similar to that which occurred in fruits punctured for the insertion of cut seeds (see p. 33).

Finally, attempts were made to determine by experiment whether an areole that had once borne a fruit could, after careful removal of this, give rise to a vegetative shoot. When from such fruits all the flowers and secondary fruits were removed, and all other areoles cauterized, and the fruits then planted in soil, no shoots at all arose from any of their areoles. This, of course, is rather to be expected, with but a single growing-point in each areole. But the latter condition had not been demonstrated histologically at the time the experiment was initiated. Then, too, it could not be assumed impossible for some of the younger, protected cells from about the margin of an areole of the primary fruit that had already produced a secondary fruit to give rise to a new-shoot growing-point, just as cells outside the areole may initiate a new-root growing-point. In a check experiment 21 fruits that had borne flowers were planted after the removal of these and no areoles cauterized. In 10 months one fruit was dead, 21 were living and rooted, and 17 of these bore shoots 3 to 4 cm. high. This demonstrated that no wound injurious to the fruit as a whole is caused by the removal of the secondary flower or fruit. On the other hand, the fact that many of the cauterized fruits mentioned took root and remained green and plump for two years demonstrates that cauterization does not seriously injure the fruit as a whole.

CAUSES AND SIGNIFICANCE OF PERENNATION AND OF THE DIVERSE TYPES OF PROLIFERATION.

We have described above the unusual persistence and secondary growth of the fruits of this opuntia and the entirely unique power of the proliferation to flowers and vegetative shoots shown by the areoles of its ovary. Beyond these facts of the structure and habit of fruit and areole lie the physiological problems of the causes and significance in the life-history of these striking peculiarities in this species of *Opuntia*.

The primary question to be answered is: Why does the fruit of this cactus never ripen like those of most cacti and of the vast majority of other angiosperms? No appreciable light on this question has been obtained from a study of this opuntia itself. Not a single fruit of this species has been seen, not even an abnormal one, that showed any indication of undergoing those changes which characterize the process of ripening in most other cacti.

The persistence, year after year, of fruits containing mature ripe seeds in attachment to the parent plant is another peculiarity entirely unexplained by observation thus far made on this opuntia. Dropping off or springing open is in the case of most plants a phenomenon closely associated with the process of ripening. The most noteworthy exception to this general rule is that of *Callistemon* and allied Myrtaceæ investigated by Ewart (1907), where the fruits persist almost indefinitely until killed by the cutting off of the water-supply by fire or drought (fig. 80).

One possible explanation of the persistent greenness and attachment of the fruit is suggested by the study of an interesting abnormal phenomenon

observed in certain other Arizona opuntias. The most striking case of those studied is afforded by *Opuntia versicolor,* a species in which the normal structure of shoot, flower, and fruit is quite similar to that found in *Opuntia fulgida.*

The fruit of *O. versicolor* is quite variable in form, size, and habit as to ripening and persistence. It may be nearly globular and from 15 to 20 mm. in diameter, as is true of most of the smaller fruits, or it may be a much-elongated structure whose whole length is 4 or 5 times its diameter (figs. 82, 84). These fruits do not soften greatly or change color with the ripening of the seeds, but remain green or yellowish during the autumn and, according to Toumey (1898), usually ripen, wither, and dry up while still on the tree during early winter. Some of the apparently normal fruits, however, as Toumey noted, may remain attached for a year or even two years. This is demonstrated by figures 82, 83, and 86, which were photographed in late April.

On examination of large numbers of these plants of *Opuntia versicolor* in April and May, it was found that most of them (about 75 per cent) bore no persistent fruits. Of those plants which did bear apparently normal persistent fruits, 9 out of 10 bore abnormal gall-like fruits also, of which we shall say more presently. It seems possible then, that the cause of the persistence of the normal fruits may be the same as the cause of the abnormality as well as of the persistence of the far more common gall fruits.

These gall fruits have an exceedingly interesting developmental history. They seem very clearly to be caused by the deposit in the flower-buds of the eggs of the cactus fly (*Asphondylia opuntiæ*). These eggs may apparently be deposited at different times in different cases, for the galls show that the flower bud has been arrested and diverted from its normal course at different phases of its development. The galls show that in some cases the arrest of normal development of the flower occurred when the perianth had hardly been initiated, in other cases after the perianth had been half-formed, and in yet others not until the perianth was fully developed (fig. 84, *a, b, c, d*).

The degree of disturbance of the normal development of the internal organs of the flower differs markedly. In some cases the stamens, pistils, and even the ovules may have been well started only to become distorted and withered without maturing, while in others no traces of stamens or ovules are to be discovered. Quite independent of these internal features are the size and external form attained by the distorted bud. Sometimes it may be no larger than some normal buds at the time of opening, while again it may reach a length and diameter twice or thrice the normal (fig. 84 *a, c*). In general external appearance most of these fruits in early April have a plump green ovary and often dark-red, waxy petals. Many of them, in fact, look precisely like gigantic, but otherwise normal flower buds that seem just ready to burst into bloom (fig. 84*d*). It is surprising that the petals can persist all winter and retain a color which though darker than the outside of

the petals is not very different from that of the inner surface of the petals in many flowers of this cactus. A section through such an abnormal flower-bud gall taken in April shows from a few to dozens or sometimes scores of the small pupæ of *Asphondylia* within the gall. They are embedded in the cortical region of the ovary, chiefly in the portion above the small ovarian cavity, and they stand perpendicular to the surface of the bud.

In spite of the rather normal appearance of many of the flower-buds which have wintered over unchanged from the preceding season, they never open to flowers. The nearest approach to this process is found in the curling open of the tips of the petals as the buds finally wither (fig. 81). The only opening of these galls that does occur is of quite a different sort. During May, especially in the latter half, the pupæ of the cactus fly transform to imagos and break out through the epidermis of the bud, each independently. The pupa-cases are left with half their length projecting beyond the surface of the gall (fig. 81). The fly itself perches on the gall while its wings are hardening (figs. 81, 84), and then flits off to play its part in infecting the new flower-buds of the season, which are then just pushing out of the areoles of the vegetative joints. By the end of May a large share of the emptied galls have withered and dropped to the ground, where they decay, often by the aid of fungi, which have ready entrance about the old pupa cases.

We come now to the consideration of the possible relation between the gall fruits or gall buds and the apparently persistent fruits. As was stated above, many of these latter fruits contain apparently good seeds. Others have only withered rudiments of seeds, and thus resemble certain of the gall fruits. In fact, a complete series of structures can be discovered grading almost imperceptibly, in both external and internal features, from typical fruits to a persistent normal-appearing flower bud. This, together with the fact that the normal type of persistent fruit in 90 per cent of the cases occurs on plants that also bear gall fruits, suggests that both have a common cause (figs. 82, 84).

If it is the presence of the egg or larva of *Asphondylia* or of some substance deposited with the egg that inhibits the normal development of the flower, but stimulates it to an abnormal and locally excessive growth and also causes it to persist over winter, then some lesser amount or degree of this same stimulus may be responsible for the persistence of the apparently normal fruits. Such stimulation might occur either by transmission of some substance or of some stimulus from an infected fruit to a neighboring one, which had not been infected. It is also possible that a fruit which had been bored for the deposit of a single egg, or a few, might continue to develop normally in every respect, except that it persisted on the tree. The only way to distinguish between these two possibilities would be by experimental study. The latter of the two views stated seems supported by the observed fact that the buds containing most pupæ are generally the ones most modified in structure, while buds or fruits with few pupæ are relatively little modified.

In other species, such as the flat-jointed *Opuntia discata,* the disturbance of the normal development of the flower and fruit by the laying of the eggs of *Asphondylia* is never so marked as in *Opuntia versicolor.* The perianth of this species is always shed, leaving a definite scar. This probably means that it develops to maturity and then opens more or less completely. The general form and size of the resulting fruit are relatively little affected (fig. 87). The ripening of the fruit also is only partially inhibited, though the complete ripening and subsequent fall of the fruit are rarely accomplished normally. In one example found at Tucson a fruit of 1913, bearing 50 or more *Asphondylia* scars, persisted and bore a vegetative joint 5 cm. long in 1914, and both were plump and green when collected in May 1915. Usually the fly escapes from its pupa-case and the riddled fruit withers as it does in *Opuntia versicolor.*

Griffiths (1913, p. 18) reports that a similar retention of the gall-like flower-buds or fruits in *Opuntia puberula* is due to the attack of the black opuntia louse.

If the explanation suggested above for the retention and modification in structure of the flower-buds of *Opuntia versicolor* is the real one for this case, then it is quite possible that a similar one may be found for the similar peculiarities of *O. fulgida.* That is, it is conceivable that some relatively slight change or lack of change in the nature of the cell-sap, or in the character of photosynthetic or other metabolic products of *Opuntia fulgida,* from a cause as simple as the sting of a fly, though as yet undiscovered, may prove the adequate explanation of the peculiarities of the fruit of this cactus. Experiments have been initiated to test this hypothesis by the aid of injections and by otherwise changing the external or internal conditions affecting the plant. They have not yet been completed.

We have still to discuss the marked diversity in behavior, under the same conditions, of the different axillary buds of the flower or matured fruit, and also that of the same buds of the fruit under different conditions. If a mature fruit of *Opuntia fulgida* is taken from the tree at any time from October to April and placed on damp soil, some of its areoles will push out to vegetative shoots. On the other hand, if the same fruit were to be left on the tree till May no shoots at all would be formed, but the same areoles might give rise to flowers instead of vegetative shoots. Moreover, while only the areoles of the distal quarter of the flower or fruit develop so long as the fruit remains attached, any of the buds, except those of the very basal quarter of the fallen fruit, may give rise to root or shoot. The areoles which actually do this are determined by the position of the fruit on the soil. Finally, if these same fruits are taken from the tree about May 1 and planted, the areoles which had already begun to swell slightly do not go on to develop vegetative shoots, but may either fail altogether to develop or give rise to small, imperfect flower-buds, which soon wither and drop off. Later, other and more basal areoles may proliferate to vegetative shoots.

The questions we have to answer here are these: Why do areoles of fruits that are picked and planted in April give rise, in the following month, to nothing but vegetative shoots when if, on the other hand, these fruits were to be left attached till May the same areoles would give rise in that month to flowers, and to these only? Secondly, what sort of change occurs in the areoles or fruit between April 1 and May 1 which makes the fruit detached at the latter date incapable of doing what it could do if detached at the earlier one? Thirdly, why do none but the most distal buds of a fruit give rise to flowers, while any but the most basal areoles of a fallen fruit may develop shoots?

In regard to the first question, it has occurred to the writer that the attached fruits give rise to flowers because these fruits and their areoles are supplied with substances—perhaps flower-forming substances—which differ markedly from those supplied to the areoles of the same fruit when it has fallen and become rooted in the ground. Or, perhaps the process of root formation may itself produce substances that inhibit flower formation in the same fruit. The plan to experiment on this by rooting attached fruits in pots of soil supported beneath them in the field has not yet been carried out. Several attached vegetative joints of a plant growing in the greenhouse at Baltimore, which from their position seemed likely to produce flowers, were rooted in pots placed beneath them. In the first season, however, these joints developed neither shoots nor fruits. It is planned to repeat this experiment on attached fruits and joints in the field at the first opportunity.

When a good-sized vegetative joint or two consecutive joints bearing several fruits is rooted in the soil, these fruits still give rise to shoot-buds only. This is true in spite of the fact that the conditions of nutrition here would be expected to be more nearly like those of fruits on a growing plant.

It was also attempted to discover by experiment whether the production of flowers alone by attached fruits is definitely influenced by the amount and kind of nutritive material available for them, in consequence of their relation to the vegetative branches bearing them and to other fruits. In each of 4 plants of *Opuntia fulgida* several branches were denuded of all fruits except 3 or 4 sets of 1 or 2 fruits each. After three seasons' growth the number of new flowers and fruits that had arisen from these undisturbed fruits was not at all abnormally increased, nor had the treatment induced the formation of a vegetative joint on a single one of the original fruits. The chief tendency of the new growth in these plants was toward the development of new vegetative joints from the old, partially denuded ones. This was most strikingly shown in a tree from which 300 fruits and 100 joints, including the top of the stem, had been lopped off and only two fertile branches with small fruit-clusters left. In this tree the new growth consisted almost entirely of vegetative joints clustered about the cut ends of the main stem and branches. In these cases, therefore, the diversion of all available nutri-

tive material of the vegetative branch into one or two fruits, instead of into several scores, did not change the fate of the areoles on these fruits. There was no increase of the vegetative activity in them such as might have been expected as a result of the increased available food-supply.

In seeking a reply to the second question proposed on page 45 it was found that all attempts made by planting very young flower-buds to induce these to become metamorphosed into vegetative shoots were unsuccessful. The evidence from these experiments seemed to show that when once the growing-point of an areole has started, even if but barely started, to form a flower, it can not be diverted and made to give rise to a vegetative shoot, as it could by removing the fruit from the plant and planting it a few weeks earlier. In every case the young flower-bud on a planted fruit either failed to develop at all or developed but slightly and then withered.

In essential agreement with these results in sprouting the detached fruits are those observed in detached vegetative joints of *Opuntia fulgida*. Fallen joints, as we have noted, very commonly take root and give rise to new plants. In no case of scores observed were flowers developed from such rooted joints until after a considerable shoot system had been formed.

In *Opuntia vulgaris,* however, a series of experiments made in May and June 1917, gave very different results. In practically every case the terminal joint or pair of joints removed just before the flower buds appear, or just after they are visible, will root promptly and then develop normal flowers and in most cases set fruit (see Hildebrandt, 1888, p. 110).

The third question raised must apparently be answered by attributing to the influence of polarity the restriction of flower buds to the most distal areoles of the fruit. This is very pronounced so long as the fruit is attached, and is definitely related to the base; that is, to the point of attachment of the fruit. In fallen fruits a much less definite polarity is exhibited which is determined by the points of origin of roots and new shoots.

Another problem suggesting itself in connection with the production of flowers from fruits is the discovery of the reason for the fact that only the terminal fruits of a cluster and a few of the subterminal ones give rise to fruits, while all the fruits basal to these, from 1 to 8 or even 10, produce no flowers. This seemed to be equally true whether this basal part of a chain bore one or several secondary or branch chains upon it. In collaboration with Dr. Hermann Spoehr, who planned the chemical side of the work, analyses were made of the pulp of the two basal fruits and the two terminal fruits of each of several chains of six or more fruits. We were unable, however, to discover any difference in the carbohydrates and other nutrient substances present in the distal flower-forming fruits and the basal sterile ones.

PROLIFERATION OF THE FLOWER OR FRUIT IN ALLIED SPECIES.

The proliferation of the ovarian wall, either in flower or fruit, has been noted in a number of other opuntias, and in at least one other genus, by Engelmann (1887), Hildebrandt (1888), and a number of more recent workers. (See also, Penzig, 1890, p. 507). Associated with this proliferation in certain cases we find a persistence of the fruits for one or more years after maturing. The areoles of the attached fruits of some of these species are known to form flowers only. The attached fruits of others, on the contrary, may develop not only new flowers and fruits, but, under certain conditions, give rise to vegetative shoots also. Of the first type are *Opuntia cylindrica, O. leptocaulis, O. catacantha,* and *Peireskia guamacho* Rose. Of the second sort are *Opuntia rufida, O. spinosissima, O. discata, O. versicolor,* and *O. arbuscula.*

Opuntia cylindrica, growing under cultivation but out of doors at Del Monte, California, frequently formed flowers by proliferation from the persistent fruits of the previous season (fig. 88). This same species also furnished striking examples of the development of first a vegetative joint and then a fruit by the uninterrupted activity of the same growing-point; that is, the joint and fruit are separated by only a very slight constriction, as was noted in speaking of *Opuntia fulgida* (*cf.* figs. 7*c,* 88). From the plants of *O. cylindrica* observed there is no evidence that the primary flowers ever give rise to buds of secondary ones before they are open.

Opuntia toumeyi, growing near Tucson, may occasionally form secondary flowers close to the base of the primary ones, which open soon after the latter.

Opuntia leptocaulis is a slender Arizona species, growing along with *O. fulgida,* in which fruits may persist unripened or half-ripened and then bud out new flowers in the succeeding season (fig. 89, *a, b, c*). These primary fruits may persist for a year and a half and the secondary ones may ripen, but tertiary fruits are rarely formed. The propagative structures here show a very closely graded series of intermediate forms between the typical fruit and the vegetative joint, a series far more complete than can usually be found on *O. fulgida* or any other near Tucson. One plant of *O. leptocaulis* seen at Chico in August bore numerous slender vegetative joints on persistent fruits of the same season and also of the preceding season.

The graded series of propagative structures above mentioned contains typical obovate fruits, with definite perianth-scars, evidently formed by normally opened flowers. Other fruits are twice as long, but still show the scar of a normal perianth. Then there are joints of various lengths, of which some bear small or very small perianth-scars while others have no scars at all, and yet all of them look very fruit-like in other external aspects. There are also many slender joints having no perianth-scars, yet closely resembling the more slender sterile fruits that do have them. None of these various structures except the shorter, obovoid ones may contain seeds, and some even

of these are seedless. Any of the sterile, fruit-like bodies may be easily dislodged and on moist ground their areoles may give rise to new plants. Such a complete series of more or less fruit-like structures might easily give the impression that these sterile propagules have arisen phylogenetically by the progressive sterilization of the normal type of fruit, accompanied by an increase in its power of sprouting from its areoles until the sterile fruits have become the chief propagative structures of this species. The plausibility of this view we shall consider in detail later (p. 52). In the meantime, however, we must remember that the so-called fruit of these opuntias is made up largely of purely vegetative elements, the internodes and the areoles and their products. It is clearly for this reason that many sterile ovaries, such as in other angiosperms (where they occur commonly) would soon wither and fall, may in *Opuntia* persist as essentially vegetative structures.

Opuntia catacantha (*O. rubescens* Salm-Dyck) is a West Indian species resembling *O. fulgida* in certain respects more closely than any other opuntia studied. It is tree-like, with very flat, paddle-shaped or scimitar-shaped joints, which in the variety studied are without spines. The fruits persist from one season to the next and then bear primary flowers of the latter season. These may bear secondary flowers and the latter form tertiary ones, and thus chains of fruits consisting of at least 6 or 8 links may finally be formed (fig. 90). These fruits vary in size, form, and internal structure. The flowers and young fruits are slender and obconical or sometimes slightly bent (fig. 90). As the fruits mature they increase considerably in size, often to about twice the original length (50 to 60 mm.) and to 4 or 5 times their original thickness. Mature fruits are often flattened until only half as thick on one transverse axis as on the other (17 by 30 mm. for example, in one shown in fig. 9). Few of the fruits have fertile seeds. None of those dissected by the writer had good seeds, but a few ripe seeds were sent him by a correspondent, the Rev. A. B. Romig, of St. Thomas, Virgin Islands.

The seed remnants found are of various sizes up to about half-grown seeds, but all are brown and withered. No definite information is available regarding the ability of these fruits to sprout to new shoots, but the fact that they are nearly always sterile suggests that they may serve as propagules just as the fruits of *O. fulgida* do. This possibility is rendered more plausible by the fact that in another spiny variety of *Opuntia catacantha* (*O. moniliformis* Haworth) collected on Mona Islands, near Haiti, by Dr. N. L. Britton, chains of short joints 1.5 by 3 cm. long are formed, which are said to sprout to new plants. These are spiny and except in size are like the regular vegetative joints. They are not pseudo-fruits like those described in *O. leptocaulis.*

In *Peireskia guamacho* is found the most striking case of proliferation of the flower that has been seen outside the genus *Opuntia,* and it appears the more remarkable because of the large bracts and long stalks of the successive flowers. In this species, as it grows in greenhouses in Washington, each

flower usually bears 4 bracts and each of these has a secondary flower in its axil. The stalks of a secondary flower may get to be a centimeter long or more and this gives the flower-cluster quite a different appearance from that of an opuntia, though its general plan is the same (figs. 92, 93). One or two, rarely more, of the flowers in such a group may develop fruits (*cf.,* Delavaud, 1858). Each globular, fleshy fruit bears a well-defined areole above each bract-scar and usually contains from one to several large, flat seeds. These seeds germinate readily, but all attempts to induce the areoles of a detached, unripened fruit to proliferate to a shoot failed. No case of the vegetative proliferation of the areole of a fruit was observed. In a similar species of *Peireskia* growing at Chico, a single parent fruit sometimes bore 5 secondary fruits and the basal secondary ones not uncommonly bore in turn tertiary fruits; that is, three generations of fruits were formed in a single season.

In the second series of species mentioned on page 47 the attached fruit sometimes proliferates to form vegetative joints as well as to give rise to flower buds. All but one of these opuntias resemble *O. fulgida* in that they form these vegetative shoots only rarely. Thus, in the flat-jointed species, *Opuntia rufida,* from Doctor Rose's collection in Washington, in *O. spinosissima* from Jamaica, and in *O. discata,* studied in the field at Tucson, the development of vegetative shoots from attached fruits occurred very infrequently (fig. 94). Hildebrandt (1888, p. 112) has reported such a case in a flat-jointed *Opuntia* growing in Freiburg. He attributed this unusual behavior to exceptionally good nutrition of the cultivated specimens. Proliferation of the fruits I found not at all uncommon in a number of the above-mentioned opuntias, and of other flat opuntias growing in the collection of Doctor Griffiths, at Chico, California (*cf.* Griffiths, 1913). In the cylindrical species, *O. versicolor,* the occurrence of such a proliferation of the attached fruit to vegetative joints is relatively very rare, only 3 or 4 cases being seen in hundreds of plants examined. In two at least of the three cases of this type observed the proliferating fruit was evidently a gall fruit (fig. 85). This fact of itself proves that these gall fruits do not always drop off during the second spring. It is doubtful, however, if they are capable, except in the rarest instances, of holding on long enough to make their vegetative offshoots an important part of the branch system. The irregularity in branching, usually resulting from proliferation of a gall fruit to a branch, should make this phenomenon discoverable several years after its occurrence (figs. 85, 86). No certain cases could be found, however, that indicated clearly the persistence of such a fruit-borne branch for more than a year or two. This sort of proliferation is practically identical with that occurring so rarely in *Opuntia fulgida,* except that in the latter the proliferating fruit is in other respects often a normal one.

On the contrary, in the round-jointed *Opuntia arbuscula,* the proliferation of attached fruits to form vegetative shoots is, under some conditions at least,

not a rarity, but a very common occurrence. The fruit of this species is persistently green, shows no sign of ripening, and not more than 5 per cent of them have well-ripened seeds. This fruit is pear-shaped, rather slender, smooth, and spineless, like that of *O. fulgida,* and has rather prominent areoles. The areoles of the primary flower very often proliferate to secondary flowers and the fruits commonly persist over one or more winters. Most of the persistent fruits are single, but chains of two are common and chains of 3 or 4 links are not infrequent. The fruits of the upper part of the rather bush-like plant seem always to produce only flowers so long as they remain attached. Many of the fruits of the lower branches, however, often give rise, from one or more up to 6 or 8 of the distal areoles, to rather slender, condensed branches, bearing numerous prominent areoles (fig. 95). These condensed branches, which may also arise on vegetative joints, are vertical in position, are about 4 or 5 mm. in diameter, and 20 to 50 mm. long. If these short branches are left on the plant they may thicken somewhat and become more like the normal, terete, vegetative shoots. No evidence was obtained, however, that the persistent fruit and its vegetative offshoot ever become incorporated into the permanent branch system of the parent plant. These condensed branches apparently play no important part in the development of this opuntia, except when the fruits or the branches alone fall to the ground, there to take root and thus start new plants.

What has been said of the proliferation of the fruits in the various *Opuntias* and in *Peireskia* indicates that each is peculiar in its own way in regard to the ripening of the fruit, in its persistence, and its proliferation to flowers or to vegetative shoots.

In the first place, the fruits of two species, *O. arbuscula* and *O. catacantha,* have fruits resembling those of *O. fulgida* in that they normally fail to ripen. The other four species, *O. cylindrica, O. leptocaulis, O. rufida,* and *O. versicolor,* apparently fail to ripen only because of some unusual condition within or about them.

Secondly, of the eight species of *Opuntia* just mentioned only two, *O. arbuscula* and *O. catacantha,* seem to resemble *O. fulgida* in having normally persistent fruits. In the others this is the less usual thing, due in all cases perhaps, as it evidently is in *O. versicolor,* to some unusual cause, such as the stimulus caused by *Asphondylia.* There are many other species also in which, as was noted by Griffiths (1913), the abnormal conditions of growth provided in cultivation frequently induce persistence of the fruits.

Thirdly, the proliferation of the areoles of the ovary to flowers, while apparently a normal occurrence in *O. arbuscula, O. catacantha,* and the closely related *O. spinosissima,* as it also is in *O. fulgida* and *Peireskia,* is a rarer phenomenon in the other four species mentioned, and in them occurs, usually, if not always, under abnormal conditions.

Finally, the proliferation of the areoles of fallen fruits to roots and shoots, thus to form new plants, may apparently occur in any of the seven opuntias, but not in the soft, quickly ripening fruits of *Peireskia.*

Taking into account all four of the peculiarities mentioned, it is clear that *Opuntia fulgida* is, on the whole, the most generally peculiar type studied, followed most closely perhaps by *O. arbuscula* and *O. catacantha*. At the other end of the graded series is *Opuntia versicolor*, which behaves like a normal angiosperm in most, or perhaps all, cases where it is not stimulated by the cactus fly, *Asphondylia*.

It is evident (from observations made in Arizona, in the cactus garden of the Bureau of Plant Industry established by Doctor Griffiths at Chico, and from records in the literature, of cases such as *Opuntia prolifera, O. cholla, O. spinosior*, etc.) that many other species of *Opuntia* fit in at various points in the series described above. In other words, in the genus *Opuntia* the ovary, in flower and in fruit, may assume now more, now fewer of the various functions of the vegetative joint. Of the *Opuntia* fruits thus far studied from this point of view, that of *Opuntia fulgida* seems not only the most atypical angiospermous fruit among these Cactaceæ, but is perhaps also the most aberrant (shoot-like) fruit to be found in all angiosperms.

PROLIFERATION OF JOINTS AND FRUITS IN RELATION TO THE STERILITY OF FRUITS.

From what has been said above of *Opuntia fulgida* it is evident that the propagation of this cactus has ceased to depend chiefly on the development of fertile seeds, and so of seedlings, but is accomplished more largely by the vegetative sprouting of fallen joints and of fallen fruits. The propagation of the species by the rooting of joints or parts of joints is rather common in several genera of Cactaceæ, such as *Cereus, Mammillaria* (Goebel, 1889), *Peireskia*, etc., in addition to many and probably most species of *Opuntia*. The propagation by means of the fallen fruit is probably common among opuntias with persistent fruits. Besides its occurrence in the forms already mentioned, it is apparently common also in *O. prolifera, O. cholla, O. spinosior*, etc.

In a number of other opuntias and certain other genera there are developed, in addition to the true fruits and ordinary vegetative joints, more specialized short joints which are often bead-like or more or less fruit-like in character. These occur, for example, in *O. arbuscula, O. catacantha, O. fulgida, O. leptocaulis, O. tetracantha* (Tourney, 1905), *Mammillaria gracilis* (Goebel, 1889), a species of *Cereus*, etc. In each case these structures are capable, after falling, of taking root in the soil and thus starting new plants.

Taking this whole series of structures, together with the various sorts of joint fruits that occur in *O. fulgida* and many other opuntias, and the many seedless opuntia fruits, it might be assumed that the fruit of these Cactaceæ, and especially of the opuntias, is losing its primary function of seed-production. It is evident at least that the production of new plantlets and the function of dissemination has been taken over in large part by these various

vegetative propagating bodies. This raises the question whether the seed-bearing fruit of all opuntias is on the way to extinction, through a progressive loss of the seed-bearing function, which may be expected to end in the evolution of a totally sterile fruit, having no propagative functions other than those that can be equally performed by vegetative joints.

It is true that the vegetative joints and both the fertile and sterile fruits resemble each other greatly in their capacity for proliferation. There seems no adequate reason, however, for assuming that either the proliferating habit or the fundamental structure of the fruit is a secondary thing in the evolution of the opuntias (Toumey, 1895). On the contrary, it is natural that the thick-skinned, water-stored joints of these cacti should prove capable of persisting on moderately moist soil until rooted deeply enough to secure a water-supply adequate for the starting of a young plant. The fruit being, as we have seen, really a stem in organization, up to the latest phase of its development, it is also very naturally capable of proliferation to root and shoot. The capacity of joint and fruit for persistence and proliferation is probably as old as the fleshy character of the family. The persistence of the sterile fruits, at least to maturity, is not a really surprising thing, in view of the preponderatingly vegetative and stem-like character of the bulk of the wall of the ovary. Sterile ovaries occur in many species of angiosperms, but in most of these the carpels constitute the bulk of the fruit. Therefore, when the seeds are wanting in these forms, and the carpels as usual fail to develop, no fruit is formed and the flower bud soon withers and drops off. In *Opuntia,* on the contrary, even if the seeds and carpellary portion of the fruit do fail to develop, the basal stem-like part may go on, practically unhindered in its vegetative growth, and mature quite normally.

When these facts concerning the comparative structure and behavior of the stem and ovary of *Opuntia* are considered, in conjunction with the fact that leaves are present on both and with the undoubted similarity of *Opuntia* to *Peireskia,* there seems no adequate reason for believing that the fruit of *Opuntia* is, structurally, an advanced type among the Cactaceæ. On the contrary, *Opuntia* and its close relative *Peireskia* (which also has a leafy ovary, the areoles of which, in the flower, proliferate to secondary flowers) probably show us the simplest type of the inferior (submerged) ovary characteristic of the Cactaceæ. The capacity of the *Opuntia* fruit for persistence and proliferation is to be regarded as the natural outcome of its original morphological composition—*i. e.,* a joint with an ovary immersed in its apex. It seems clearly not a result of a marked degeneration of a once less stem-like and more constantly fertile fruit, such as has been assumed by some investigators to have been present during the evolution of the genus. The more specialized or highly evolved flowers and fruits, structurally, among the Cactaceæ are probably to be sought in such genera as *Cereus, Rhipsalis,* and *Mammillaria.*

SUMMARY AND CONCLUSIONS.

The fruits of certain opuntias differ from those of other angiosperms, except those of some Australian "bottle-brush" trees, in not ripening and then either opening or falling from the plant when the seeds are mature. On the contrary, the peculiar fruits of these Cactaceæ and Myrtaceæ remain attached to the plant and actively growing for several or many years.

The persistent fruit of *Opuntia fulgida* is still more abnormal in another respect, for it not only remains attached, unripened and steadily growing, season after season, but the seeds are never shed from the fruit. Furthermore, the matured fruit itself, or even the ovary of the unopened flower, while still attached to the tree, may give rise to secondary flowers and so to other fruits. Four or five generations of flowers and fruits may thus be formed in a single season. Finally, if a mature fruit falls on moist soil it may develop adventitious roots and shoots and thus initiate a new plant.

This tree-like opuntia has a tuberculate and spiny cylindrical stem and branches, the fleshy joints of which on separation readily sprout to new plants.

The early development of the ovary of the flower in *Opuntia fulgida* closely resembles that of a young vegetative joint, and the structure resulting from this early development, with its minute, evanescent leaves, its tubercles, and axillary areoles, is entirely stem-like in appearance. Only with the initiation of the perianth, stamens, and carpels does the fertile joint become distinctly flower-like in character. The ovarian cavity finally becomes completely buried in the stem-like, basal portion of the ovary, by the more rapid growth of this portion upward and inward about the base of the carpels. The whole outer wall of the ovary and fruit is thus a stem in its morphological origin. This is clearly indicated not only by the more general features of development noted, but also by the identity in details of development and structure of the tubercles and areoles, and of the photosynthetic and water-storing tissues in the stem and fruit. In its physiological capacity for persistence and for proliferation to flowers and shoots, the wall of the fruit shows again its essential identity with the stem. Finally, the graded series of structures intermediate in character between joint and fruit, serve to further emphasize the likeness of the two.

The development of the flower of this opuntia indicates that it has evolved from one with an originally superior ovary through the progressive submergence of this ovary by the more vigorous growth of parts of the fertile joint that were laid down before the carpels themselves were even initiated. This is probably a relatively primitive type of flower among the Cactaceæ, from which the type found in *Cereus* and *Echinocactus* has been derived.

The perianth, the stamens, and the style are cut off from the top of the ovary, a day or two after the flower withers, by the formation of a highly developed, cup-shaped abscission layer. Any cells of the fruit except those

of the vascular bundle may participate in the formation of the cells of the abscission layer. The cells of the vascular bundle in line with the abscission layer seem to degenerate and rupture as a result of the split in the adjoining tissues. The whole funnel-like scar left at the top of the ovary by the fall of the perianth is soon protected by several layers of periderm. These arise from a phellogen formed but a few layers within the abscission layer. One, or sometimes several, layers of this periderm may have the cell-walls greatly thickened to form a schlerenchymatous protective layer.

From the axillary buds, or areoles, of the primary flowers that open in May, arise secondary flowers which open in June. From areoles of these, in turn, tertiary flowers open in July, and on the latter quaternary flowers bloom forth in August. Thus four and sometimes five generations of flowers may be formed each season. Often two or three and sometimes four generations of persistent fruits may thus arise in a single summer.

The number of well-matured seeds occurring in a fruit may range from 0 to 100 or even 200. Large numbers of sterile seed-rudiments of various sizes are found in most fruits, some of them evidently having degenerated soon after their initiation. The fertile seed contains a large coiled embryo and a small mass of endosperm in the loop between radicle and cotyledons. The seeds of this opuntia have not, so far as is recorded, been known to germinate in the field under natural conditions. They were germinated in the laboratory by slightly chipping the seed-coat. The seeds may remain unchanged and capable of germination for several or many years while embedded in the pulp of the persistent, attached fruits, or even in that of fallen, rooted ones. The seeds are set free in nature only by the decay of the pulp of the fallen fruit, or when the fruits are eaten by browsing animals. It is possible that the failure of the seeds to germinate in the moist pulp of the fruit, even during the hot summer, may be due to the impenetrability of the seed-coat. Even chipped seeds, however, do not germinate in this medium as they do in soil or on wet filter-paper, which suggests that the pulp may have an inhibitory effect on some process connected with germination.

The mature fruit, unripened, remains attached to the tree after the ripening of the seeds. It may thus persist and grow year after year, by the aid of a cambium ring. It is this persistent fruit that gives rise to flowers, just as a stem would. By the proliferation of the primary flowers, so formed, secondary and tertiary flowers arise and develop to persistent fruits, two, three, or even four generations per season. In the course of several years a cluster may arise containing scores of fruits with sometimes 10, 12, or even 14 generations of fruits in a continuous linear series.

Only in two cases, among hundreds examined, were attached fruits found proliferating to vegetative joints.

Fallen fruits that rest on moist ground may give rise to adventitious roots, from areoles, perianth-scar, or stalk-scar, and then to vegetative shoots, from areoles only, and thus initiate new individual plants. In nature this origin

of new plants from fallen fruits is the most important means, next to proliferation of fallen joints, of the multiplication and dispersal of this cactus.

The difference between the product of an areole of an attached fruit and one of a fallen fruit that has rooted seems probably due to a difference in the kind of nutritive (organ-building) material brought to the two areoles under these different conditions. It is possible that the presence of roots on the fallen fruit inhibits the formation of flowers by it.

Persistence and proliferation of the fruit, though not elsewhere as frequent as in *Opuntia fulgida,* is not unknown in other species. In *Opuntia versicolor,* as also in several flat-jointed opuntias, the frequent persistence of the fruit or even of the unopened flower is the result of the puncture of the flower-bud by the cactus fly, which lays its eggs in it. In other cases, like *O. catacantha,* the factors that inhibit ripening and induce persistence are as undetermined as they are in the case of *O. fulgida.*

The fact that *Opuntia fulgida* and other species have series of fruits showing various degrees of sterility, from those with scores of seeds to those that are entirely seedless, can not be taken as conclusive evidence that seed-production is really on the way to complete extinction in these plants. Neither is the corollary that propagation by seeds is being replaced by the proliferation to new plants of fallen fruits as significant as it might at first seem. On the contrary, the stem-like character of the fruits in this genus results in the persistence of many sterile ovaries, such as would, in many less fleshy angiosperms, wither and fall off soon after blooming, instead of maturing into seedless fruits, as they do here.

LITERATURE CITED.

CASPARI, H. 1883. Beiträge der Kenntniss des Hautgewebes der Cacteen. Zeit. für Naturwiss., 2, pp. 30–80.

CROCKER, W. 1906. Rôle of Seed-coats in Delayed Germination. Bot. Gaz., 42, pp. 265–290.

DARBISHIRE, O. V. 1904. Observations on *Mammillaria elongata*. Ann. of Bot., 18, pp. 375–416.

DEBEY, M. H. 1846. Proliferation d. Fruchtknotens lieferte eine *Opuntia Salm-Dyckiana*. Verhandl. d. Naturhist. Ver. Preuss. Rheinl., 3, 83, 84.

DELAVAUD, M. C. 1858. Inflorescence du *Peireskia bleo*. Bull. Soc. Bot. de France, 5, p. 685.

DELBROUCK, C. 1875. Die Pflanzenstacheln. Hanstein Botan., Abhandl. 2, pp. 1–119.

ENGELMANN, W. 1887. "Cactaceæ of the Boundary," in Botanical Works. Edited by W. Trelease and Asa Gray. Cambridge. p. 212.

EWART, A. J. 1907. The Delayed Dehiscence of *Callistemon rigida*. Ann. of Bot., 21, pp. 125–137.

GANONG, W. F. 1894. Beiträge zur Kenntniss der Morphologie und Biologie der Cacteen. Flora, Ergänzungsb., pp. 49–86.

———. 1898. The Comparative Morphology of the Embryos and Seedlings of the Cactaceæ. Ann. of Bot., 12, pp. 423–474.

GOEBEL, KARL. 1886. Zur Entwickelungsgeschichte des Unterständigen Fruchtknotens. Bot. Zeit., 44, pp. 729–738.

———. 1889. Pflanzenbiologischeschilderungen. I. Kakteen, pp. 67–108.

GRIFFITHS, D. 1913. Behavior, Under Cultural Conditions, of Species of Cacti Known as *Opuntia*. Bull. No. 31, U. S. Depart. of Agricult.

HARRIS, J. A. 1905. The Fruit of *Opuntia*. Bull. Torrey Bot. Club, 32, pp. 531–536.

HILDEBRANDT, F. 1888. Ueber Bildung von Laubsprossen aus Blüthensprossen bei *Opuntia*. Ber. d. deutsch. bot. Gesellsch. 6, pp. 109–112.

KAUFFMANN, N. 1859. Zur Entwickelungs. d. Cactaceenstacheln. Bull. Soc. Imp. des Naturalistes de Moscow, 32, part II, pp. 585–603.

LAUTERBACH, C. W. 1889. Untersuchungen über Bau und Entwickelungs der Sekretbehälter bei des Cacteen. Bot. Centrbl., 37, p. 257.

LLOYD, F. E. 1907. Observations on the Flowering Period of Certain Cacti. Plant World, 10, pp. 31–39.

———. 1916. Abscission in *Mirabilis jalapa*. Bot. Gaz., 61, pp. 213–230.

MEEHAN, T. 1888. *Opuntia* Fruits. Gard. Chron., 3, p. 328.

NOLL, F. C. 1872. Zwei Abnormitäten an Cactusfrüchten. Ber. d. Senckenbg. Gesell., 1872, p. 118.

PENZIG, O. 1890. Pflanzenteratologie. Genoa.

SCHLEIDEN, M. J. 1845. Beiträge zur Anatomie des Cacteen. Mem. l'Acad. Imp. d. Sci. d. St. Petersb., ser. 6, vol. 4, pp. 335–380.

SCHUMANN, K. 1894. "Cactaceæ." Engler u. Prantl, III, 6*a*, pp. 156–205.

———. 1890. Flora Brasiliensis, IV, 2.

SOLEREDER, H. 1908. Systematic Anatomy of the Dicotyledons. Engl. Transl., pp. 406–415.

TOUMEY, J. W. 1895. Vegetal Dissemination in *Opuntia*. Bot. Gaz., 20, pp. 356–361.

———. 1898. The Tree Opuntias of the United States. Bot. Gaz., 25, pp. 119–124.

———. 1905. Notes on the Fruits of Some Species of *Opuntia*. Bull. Torr. Bot. Club, 32, pp. 235–239.

WETTERWALD, X. 1889. Blatt- und Sprossbildung bei Euphorbien und Cacteen. Nova Acta Kaiserl. Leopold. Carol., Ak. 53, pp. 379–440.

WOLFE, F. A. 1912. Notes of the Anatomy of *Opuntia lindheimeri*. Plant World, 15, pp. 294–298.

ZUCCARINI, J. G. 1836. Plantarum novarum vel minus cognitarum, etc. Fasc. tertius, Cactaceæ. Abhandl. Muench. Akad., Math. physik. Klasse, 2, pp. 599–742.

EXPLANATION OF PLATES.

ABBREVIATIONS USED IN PLATES.

a., areole or cushion formed by axillary bud; *a. l.*, abscission layer; *b.*, bristle or glochidium; *bb.*, barb of bristle or of spine; *c.*, carpel; *ck.*, cork; *cm.*, cambium; *c. c.*, crystal containing cell; *c. t.*, conducting tissue of style; *c. w.*, cell-wall; *e.*, epidermis; *em.*, embryo; *ep.*, endosperm; *f.*, flower; *fu.*, funiculus or stalk of ovule; *g. c.*, guard-cell; *g. p.*, growing-point; *h.*, hypodermis; *i.*, integument; *l.*, leaf; *l. s.*, leaf-scar; *n.*, nectary; *o.*, ovary; *ov.*, ovule; *p.*, petal; *ph.*, phellogen; *pl.*, palisade; *p. s.*, perianth-scar; *r.*, root; *s.*, sepal; *sa.*, stamen; *s. c.*, slime-cell; *sd.*, seed; *sg.*, stigma; *sh.*, sheath of spine; *so.*, stoma; *sp.*, spine; *st.*, stem; *sy.*, style; *t.*, trichome; *tb.*, tubercle; *v. b.*, vascular bundle; *w. f.* wall of fruit.

Frontispiece.

Photograph of a mature plant of *Opuntia fulgida* on reservation of Desert Laboratory at Tucson, showing a frequent type of forked trunk, due to injury of main axis, also the branching habit and clusters of fruit. The nesting bird is the cactus wren, *Heleodytes brunneicapillus couesi* (Sharpe). [D. T. MacDougal photo.]

Plate 1. Photographs of Opuntia fulgida.

Fig. 1. A fruiting plant growing in the desert at Tucson. Photographed April 25, 1915. × 0.03.

Fig. 2. Heavily fruiting branches of a tree on the campus of the University of Arizona. The largest cluster included more than 100 fruits. Photographed in May 1912. × 0.1.

Fig. 3. A single large cluster of fruits from the same tree as figure 2. × 0.3.

Fig. 4. A vegetative joint and fruits of 1914 bearing buds of flowers of 1915. Photographed in May 1915. × 0.6.

Plate 2. Photographs of O. fulgida.

Fig. 5. Tip of a vegetative joint with young joints still bearing the evanescent leaves, showing also areoles with spines and nectaries. × 0.9.

Fig. 6. Four generations of flowers and fruits developed from a vegetative joint in the season of 1915. This cluster, collected at Tucson and photographed in mid-July 1915, shows the relative sizes of the four generations. No. I opened in May; II in June; III, if not removed from the plant, would have opened in late July; IV in late August. Note that some members of generation III (at right below) have but barely pushed out of the areole. × 0.6.

Fig. 7 *a*, *b*, *c*. Joint-fruits and pseudo-fruits, showing several structures combining in various degrees the characters of vegetative joint and fruit. × 0.45.

Fig. 8. Cluster of 11 secondary fruits borne on a single primary fruit showing the persistence of fruits over one, two, or more winters. Photographed April 1915. × 1.

Fig. 9*a*. Joint of 1914 bearing opened and withered flower of 1915, the latter with buds of secondary flowers on its sides. × 0.6.

Fig. 9*b*. Similar joint bearing primary flowers. In the areoles of these are borne trichomes, nectaries, and buds of secondary flowers. Many of the latter bear numbers of the awl-shaped deciduous leaves. × 0.6.

Plate 3. Drawings of O. fulgida.

Fig. 10. Radial section of an axillary bud of flower, showing growing-point, nectary, spine, etc. × 25.

Fig. 11. Longitudinal section of a flower bud through a placenta, mammillæ, leaves, two axillary buds, a nectary, etc. × 3.33.

FIG. 12. Enlarged drawing of the areole shown at left in figure 11. It would probably have developed a flower if it had been left on the plant. × 25.

FIG. 13. Part of a longitudinal and radial section of an unopened flower, bearing the very young bud of a secondary flower at right. × 5.

FIG. 14. Longitudinal section of a young flower bud arising from the edge of the perianth-scar on the fruit of the preceding season, showing leaves, very prominent tubercles, and growing-points of the areoles on the adaxial faces of the latter; showing also the shriveled nectaries developed in the preceding season. × 12.

FIG. 15. Longitudinal section of a slightly older flower than that shown in figure 14, showing the depression of the growing-point and the initiation of the stamens. × 18.

FIG. 16. Longitudinal section of a still more advanced flower, showing the much sunken growing-point and three series of stamens on each side of it. × 18.

FIG. 17. Longitudinal section of flower with all stamens and carpels initiated. The two upper areoles now face upward instead of axially. × 9.

FIG. 18. Part of a longitudinal section of a young flower showing further closing in of the carpels above the cavity of ovary to form stylar canal. × 24.

FIG. 19. Longitudinal section of upper part of a slightly older flower, showing style with free tips that are to form stigmas. × 17.

FIG. 20. A section, similar to that in figure 19, of a flower in which the placentæ are just distinguishable; at base of nectary at left is a leaf-scar, and below the nectary is the vascular bundle that led to leaf. × 8.

FIG. 21. Longitudinal section of a half-matured flower, showing ovules just initiated, stamens differentiated to anther and filament, etc. × 5.

FIG. 22. Longitudinal section of a flower nearly ready to open, showing ovules, style with its conducting tissue, the papillose stigmas, and tightly overlapped sepals and petals. × 4.5.

PLATE 4. DRAWINGS OF O. FULGIDA.

FIG. 23. Longitudinal section of a flower that has just commenced to open, showing ovules, papillose recurved stigma-lobes, etc. × 4.

FIG. 24. Longitudinal section of a young fruit from which the perianth and stamens have recently fallen, showing the funnel-shaped scar with its corky lining layer. × 3.

FIG. 25. Longitudinal section of a primary fruit with ripe seeds bearing a secondary fruit, showing relative size of fruits and degree of development of seeds, the connection of vascular systems, etc. × 1.5.

FIG. 26. Longitudinal section of two matured fruits, one or two years old, with aborted seeds of various sizes, though fruits are plump and normal in external form. × 1.25.

FIG. 27. Longitudinal section of a mature fruit, showing the usual shape of fruit, its perianth-scar, areoles, and vascular system, also ripe seeds, together with other seeds that have withered at various stages of development. × 1.25.

FIG. 28. Longitudinal section of a combination joint fruit, one or two years old, showing the relatively small portion of its length occupied by the ovarian cavity, which in this case contained only half-matured withered seeds; showing also the vascular system and the prominent tubercles, the one at the right with two spines. × 1.5.

FIG. 29. Transverse section of young flower bud showing petals, sepals, leaves, and at left one spine. × 10.

FIG. 30. Transverse section of same bud lower down, showing the six stigmas, petals, sepals, leaves, and the very prominent tubercles with their areoles; showing nectaries, spicules, etc. × 5.

FIG. 31. Transverse section of the bud shown in figure 29, at level of the styles and stamens. × 5.

FIG. 32. Transverse section of the bud shown in figure 29, at level of the ovarian cavity, showing first rudiments of ovules. × 5.

FIG. 33. Transverse section of the sterile base of the same flower bud as that shown in figure 29, showing the ring of vascular bundles, with fascicular cambium already established. × 5.

FIG. 34. Transverse section of an older flower bud through seven styles or stigmas, the stamens, petals, and sepals. × 5.

FIG. 35. Part of an approximately transverse section of the flower shown in figure 34, giving details of structure of style and stigma, including the papillose lining of the stylar canal. × 20.

PLATE 5.

FIG. 36. Part of transverse section of a stigma, showing papillose surface, and the conducting tissue, vascular bundle, slime-cells, etc., within. × 75.

FIG. 37. Transverse section through the flower shown in figure 34, showing style, stamens, and wall of ovary with its tubercles, areoles, etc. × 3.

FIG. 38. Part of transverse section of young ovary, showing long-stalked ovules with integuments initiated, and archesporial cell differentiated. × 24.

FIG. 39. Transverse section of a young ovary, showing seven placentas with numerous anatropous ovules, also the vascular structure and radial arrangement of photosynthetic cells in tubercle. × 4.

FIG. 40. Transverse section of slightly older ovary, showing the filling up of the ovarian cavity by the growth of the young ovules and their stalks. Note that the magnification is but half that of figure 39. × 2.

FIG. 41. Transverse section of mature ovary showing two nearly ripe seeds and a larger number of sterile seeds that have ceased growing at various stages of development. × 2.

FIG. 42. Transverse section of a persistent, fertile fruit several years old, showing seeds and their stalks completely filling ovarian cavity, the great radial growth of the vascular bundles, and the loss of prominence of the tubercles. × 2.

FIG. 43. Transverse section of the sterile base of a fruit like that of figure 42, showing the large central mass of water-filled parenchyma, the radial growth of the vascular bundles from the activity of the fascicular cambium, and the generally smooth, rounded outline of the surface. × 2.

FIG. 44. Transverse sections of vascular bundles from ovaries of various ages, all at same magnification, to show relative growth of the phloem and xylem regions of the bundle. (*a*) From ovary of a flower from which the perianth has just fallen; (*b*) from one-year fruit; (*c*) from a fruit 6 or 8 years old, 35 millimeters in diameter. × 11.

FIG. 45. Transverse section of lower third of nearly mature leaf from the ovary of a flower about ready to open, showing flattened form, vascular system, slime-cells, and the slightly specialized palisade. × 42.

FIG. 46. Transverse sections near tip of leaf from flower bud, showing small vascular strand, slightly developed palisade, and large air-canals. × 50.

FIG. 47. Surface view of a flower bud some time before opening, showing sepals and petals and six areoles. Two of the latter have already initiated flower buds, in which the spindle-shaped leaves of lower part of ovary and the flattened sepals and petals can be distinguished. Each of the remaining areoles shows a leaf-scar and the dense tuft of trichomes, with its inner border of spicules and its one or several embedded nectaries. × 3.

PLATE 6.

FIG. 48. Part of transverse section near top of opening flower, showing upper surface of an areole and a cross-section of the subtending leaf. Among the trichomes of the areole are ten nectaries, and about its inner border is a group of a dozen or more bristles or glochidia. × 2.

FIG. 49. Part of a transverse section of a recently opened primary flower, showing edge of cup of flower and three tubercles, one of them bearing an areole with two nectaries and the bud of a secondary flower. The arrow indicates the sagittal plane. × 3.

FIG. 50. Radial or sagittal section of an areole of a primary flower, showing the growing-point or stem apex of the areole, its bordering groups of bristles and trichomes, two nectaries, and the subtending leaf. × 18.

FIG. 51. Three typical trichomes from an areole, showing their swollen tops and slender bases. × 45.

FIG. 52. A single trichome from an areole, showing thick-walled pitted cells of tip. × 110.

FIG. 53. A mature spine, showing the swelling at base, the barbed tip, and the transparent sheath attached for its lower sixth, while the upper five-sixths of it is loose and has slipped down by splitting and folding near the base to leave the tip of the spine exposed. × 5.

FIG. 54. The upper fourth of an immature spine, showing in detail the intact striated sheath and the barbed tip of the spine itself. × 50.

FIG. 55. Transverse section of a spine from a young fruit, showing the sheath of loosely packed hairs and the spine with its core of closely compacted small cells and its outer layers of large thick-walled barb-cells. × 110.

FIG. 56. Part of a sagittal section of an areole, showing a nectary with bristles and trichomes at its base, with the separated, cutinized layer of the epidermal cells at its tip; also the vascular supply of the nectary and of the subtending leaf. The leaf is just being cut off to leave a relatively small leaf-scar. × 45.

FIG. 57. Surface view of upper half of a mature spicule or glochidium, showing the barbs closely resembling those of spines. × 72.

FIG. 58. Longitudinal section of basal fourth of a nearly mature bristle, showing internal structure, barbs, and zone of rupture at which bristle breaks off. × 125.

FIG. 59. Transverse section near middle of an immature spicule, showing the large, thickened surface cells which are to give rise to the barbs. × 225.

FIG. 60. Longitudinal section of upper half of opening flower, showing the most frequent location of the abscission layer, which cuts off the whole perianth from ovary, but leaves style to be cut off independently. × 3.

FIG. 61. Section similar to that in figure 60, showing another type of abscission layer, which cuts off the style as well as the perianth. Separation has already occurred in the left half, while the abscission cells on the right are in the stage shown in figure 67. × 3.

FIG. 62. Part of longitudinal section of wall of an ovary from which the perianth has fallen, showing surface left after the break through the youngest cells of the abscission layer. The arrow is parallel to the basal part of the style. (*Cf.* figure 67.) × 48.

FIG. 63. Part of radial section of perianth-scar of very young fruit, showing phellogen layer and cork. Abscission surface at right. × 117.

FIG. 64. Part of radial section of perianth scar of a two-year old fruit, showing the parenchyma of fruit at left, phellogen in the middle, and cork at right. × 110.

FIG. 65. Small portion of section similar to that in figure 64, showing structure of two of the thickened cells in the cork. × 225.

FIG. 66. Outline of vascular system of inner petal. × 5.

PLATE 7.

FIG. 67. Part of the radial section of ovary of newly opened flower illustrated in figure 59, showing various stages in the division of cells that are forming the abscission layer. The arrow is parallel to the style. × 110.

FIG. 68. Part of radial section through ovary of an opening flower, showing the relation of the abscission layer to the vascular bundles and to the mucilage cells. × 19.

FIG. 69. Part of transverse section of two-year vegetative joint, taken through a tubercle just below its areole, showing the structure of the epidermal and of the palisade-like chlorophyll-containing tissues of the stem. × 45.

FIG. 70. Transverse section of a two-year vegetative joint, at about 2 centimeters above base, showing vascular bundles and the radiate arrangement of the palisade tissues in each tubercle. (*Cf.* figures 39 and 43.) × 1.5.

FIG. 71. Part of transverse section of tubercle of an unopened flower, showing epidermis, stomata and palisade with its intercellular air spaces. × 205.

FIG. 72. Small portion of transverse section of two or three year old fruit, showing details of stomata of the epidermis and its thick-walled underlying layers. × 365.

FIG. 73. Small portion of transverse section of tubercle of similar fruit, showing resemblance of the palisade, etc., to that of the vegetative joint. (*Cf.* figure 69.) × 110.

FIG. 74. Part of tangential section of tubercle of a two-year vegetative joint, showing palisade cells and mucilage cells in cross-section. × 85.

FIG. 75. Section of one of the crystal-holding cells so abundant in the subepidermal and parenchymatous tissues. × 365.

PLATE 8. PHOTOGRAPHS 76 TO 79, O. FULGIDA; 80, CALLISTEMON; 81, O. VERSICOLOR.

FIG. 76. Lateral view of a five months' seedling, showing hypocotyl, cotyledons, and first joint of stem. Seed planted April 27, 1917; photograph of living seedling made October 12 following. × 0.9.

FIG. 77. Part of a cluster of fruits collected at Tucson in April 1915, showing one chain of 14 links in a single linear series. × 0.3.

FIG. 78. Plantlet 10 months old, developed in a greenhouse in Baltimore from a fallen fruit, showing position of adventitious roots and structure of the new shoots. × 0.66.

FIG. 79. One of the two examples found in which the persistent fruits of *O. fulgida*, while still attached, proliferate to vegetative branches. Collected and photographed at Tucson in April 1915. × 0.45.

FIG. 80. Branch of *Callistemon speciosum*, with three generations of flowers and fruits, showing the persistence and growth of the firm green capsules. Flowers at the tip about to open. Collected on the campus of the University of California in March 1916. × 0.23.

FIG. 81. Gall fruit of *O. versicolor*. Collected and photographed at Tucson in April 1915, showing the curling of the abortive petals and the fly *Asphondylia*, which has just escaped from one of the pupa cases projecting from the side of the gall below the fly. × 0.3.

PLATE 9. PHOTOGRAPHS OF O. VERSICOLOR.

FIG. 82. A branch of *O. versicolor* bearing several clusters of fruits and galls of 1914, and groups of flower buds of 1915. Some of fruit-like structures are clearly galls, but others are nearly, if not quite, normal. Collected and photographed at Tucson, May 1915. × 0.45.

FIG. 83. A piece of a vegetative joint of *O. versicolor* collected at Tucson in April 1915, showing 3 types of persistent fruits or galls. × 0.6.

FIG. 84. Four types of gall fruits of *O. versicolor*, showing, at left, a slightly developed perianth; and, at right, a very highly developed perianth. Collected and photographed at Tucson in April 1915. × 0.45.

FIG. 85. Branch of *O. versicolor* with two galls of 1913 or 1914. One of these bearing two vegetative branches developed in 1914, and each of these a cluster of flower buds for 1915. Collected and photographed at Tucson in May 1915. × 0.45.

FIG. 86. Branch of *O. versicolor*, showing persistent fruit (normal?) bearing a vegetative branch which is directed backward toward base of the parent branch. Tucson, April 1915. × 0.45.

PLATE 10. PHOTOGRAPHS OF O. DISCATA, O. CYLINDRICA, O. LEPTOCAULIS, AND O. CATACANTHA.

FIG. 87. Portion of joint of *O. discata* bearing a gall fruit with projecting pupa cases from which the cactus flies have just escaped. × 0.45.

FIG. 88. Tip of a joint-fruit of *O. cylindrica* of 1913, bearing a persistent fruit of 1914, two flowers and a vegetative joint of 1915. Note constriction only, instead of the usual distinct articulation at base of the parent fruits. × 0.45.

FIG. 89, *a*, *b*, *c*. Three branches of *O. leptocaulis* bearing fertile fruits of 1914, sterile fruits, various forms of more or less fruit-like branches, and also (*c*) flower buds for 1915. × 0.45.

FIG. 90. A single joint of *O. catacantha* bearing four chains of fruits (all sterile), showing one chain of six links on right and a single open flower on left. Collected at St. Thomas, Virgin Islands, May 1915. × 0.45.

FIG. 91. Series of fruits of *O. catacantha* (from same collection as those in figure 90) in surface view, also in longitudinal and transverse section, showing perianth-scar and small sterile ovarian cavity. × 0.45.

PLATE 11. PHOTOGRAPHS OF PEIRESKIA, OPUNTIA RUFIDA, O. ARBUSCULA, AND O. LEPTOCAULIS.

FIG. 92. Two generations of flowers of *Peireskia guamacho*, showing proliferation of primary flower from axillary buds at the level of the ovarian cavity (indicated by an *x*). The primary flower and the secondary one at right are shown in median longitudinal section. × 0.6.

FIG. 93. Flower and fruit of *Peireskia guamacho*, showing umbilicate fleshy fruit with areole on right side above. × 0.9.

FIG. 94. A joint of *O. rufida* bearing three persistent fruits, from one of which a new vegetative joint has arisen. × 0.45.

FIG. 95. Two lower branches of *O. arbuscula* bearing persistent fruits, and these, as well as the normal vegetative joints, bearing slender condensed shoots with closely packed areoles. × 0.45.

FIG. 96. Branch of *O. leptocaulis* showing fruits and fruit-like branches, like those described for figure 89. × 0.45.

PLATE 12. DRAWINGS OF O. FULGIDA.

FIG. 97. Tangential section of half-grown seed, perpendicular to the flattened sides of seed and passing through micropyle, showing pocket of funiculus which incloses the seed and the two integuments. × 95.

FIG. 98. Section of ripe seed in plant of greatest diameter, showing embryo, endosperm, integuments, and thick wall of funicular pouch with its included vascular bundle. × 17.

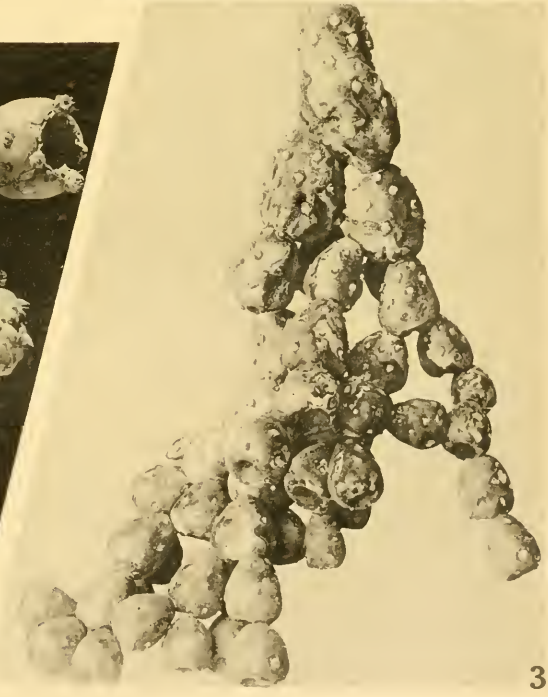
FIG. 99. Longitudinal section of a fruit which has given rise to a new plantlet, showing the portion of the fruit cut off by a layer of cork from participation in the new plant. × 1.33.

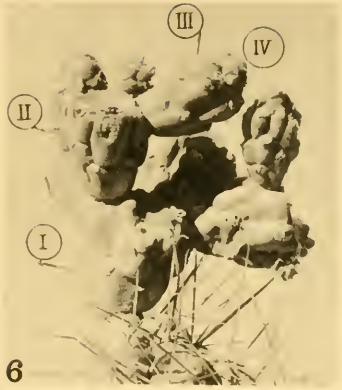
FIG. 100. Longitudinal section of a fallen fruit through the point of origin of an adventitious root from the border of an areole. × 14.

2

1

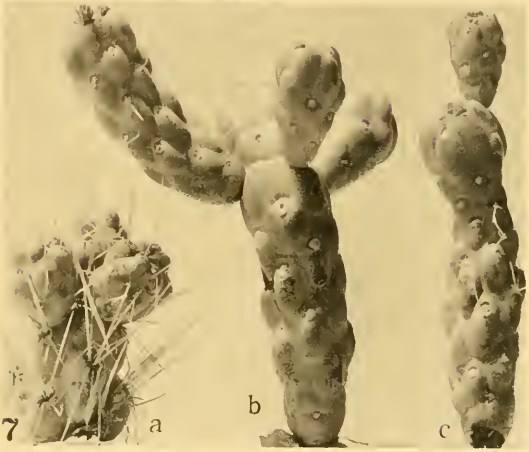
4


3



6

5

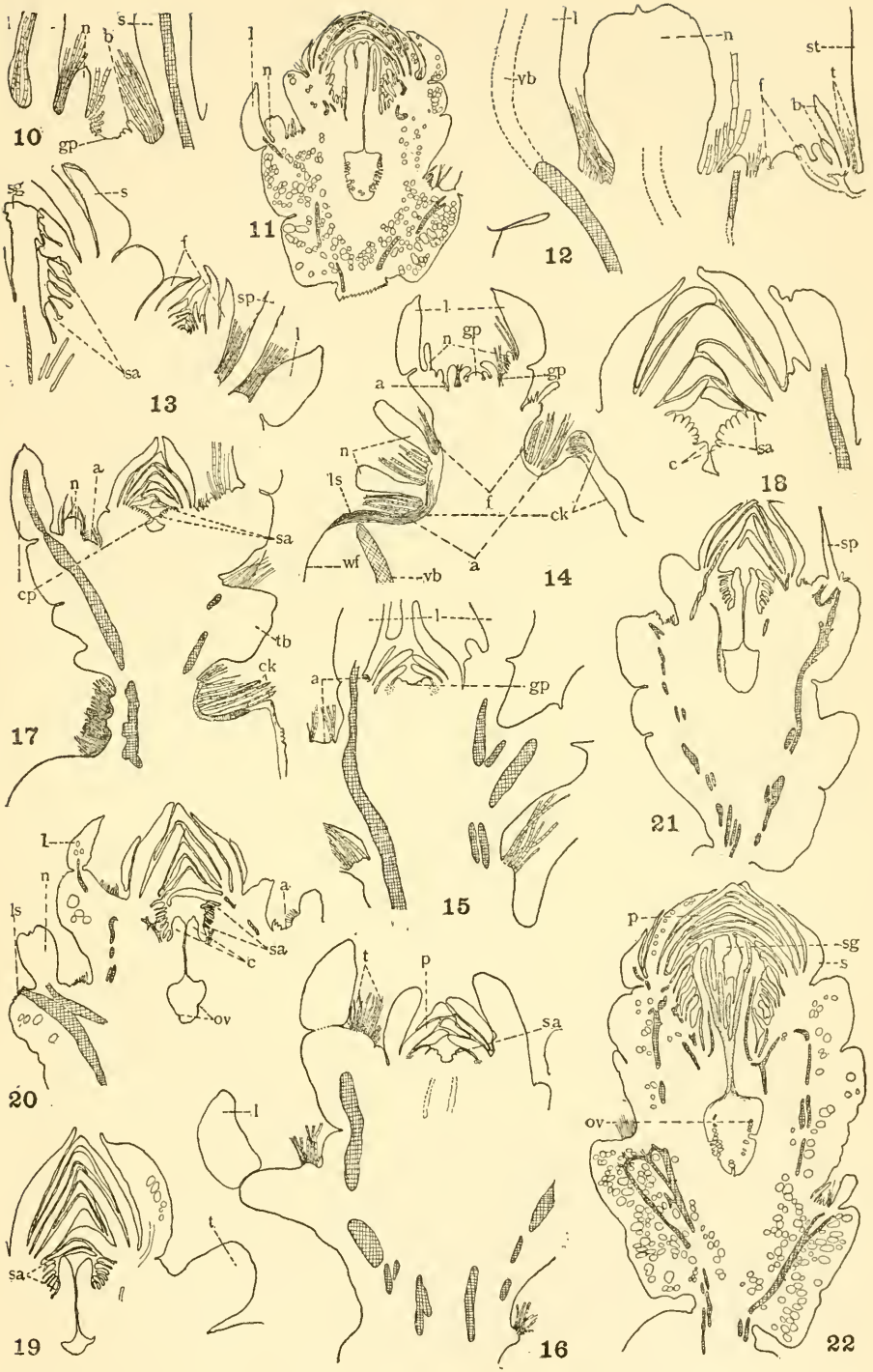


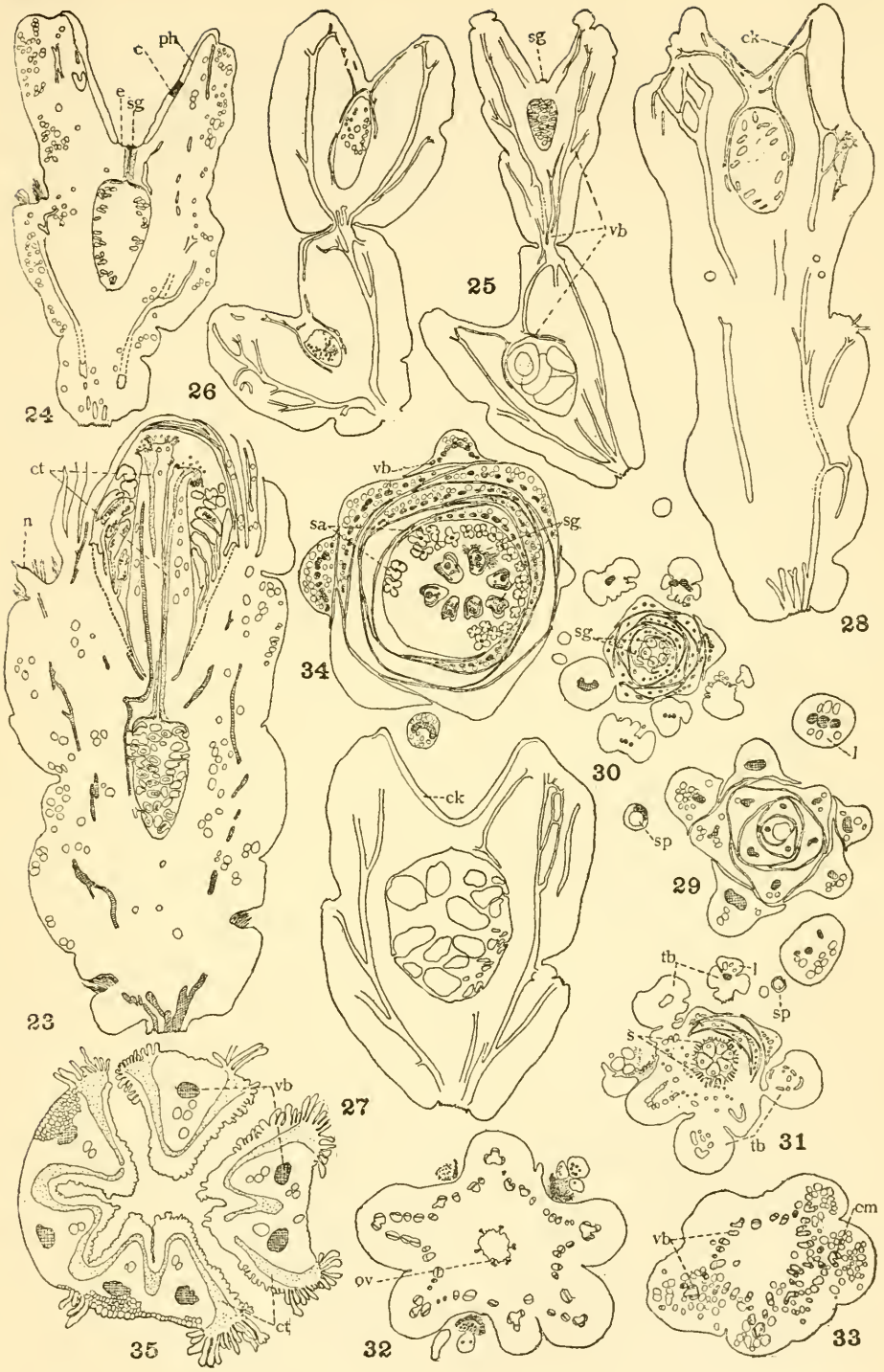
7

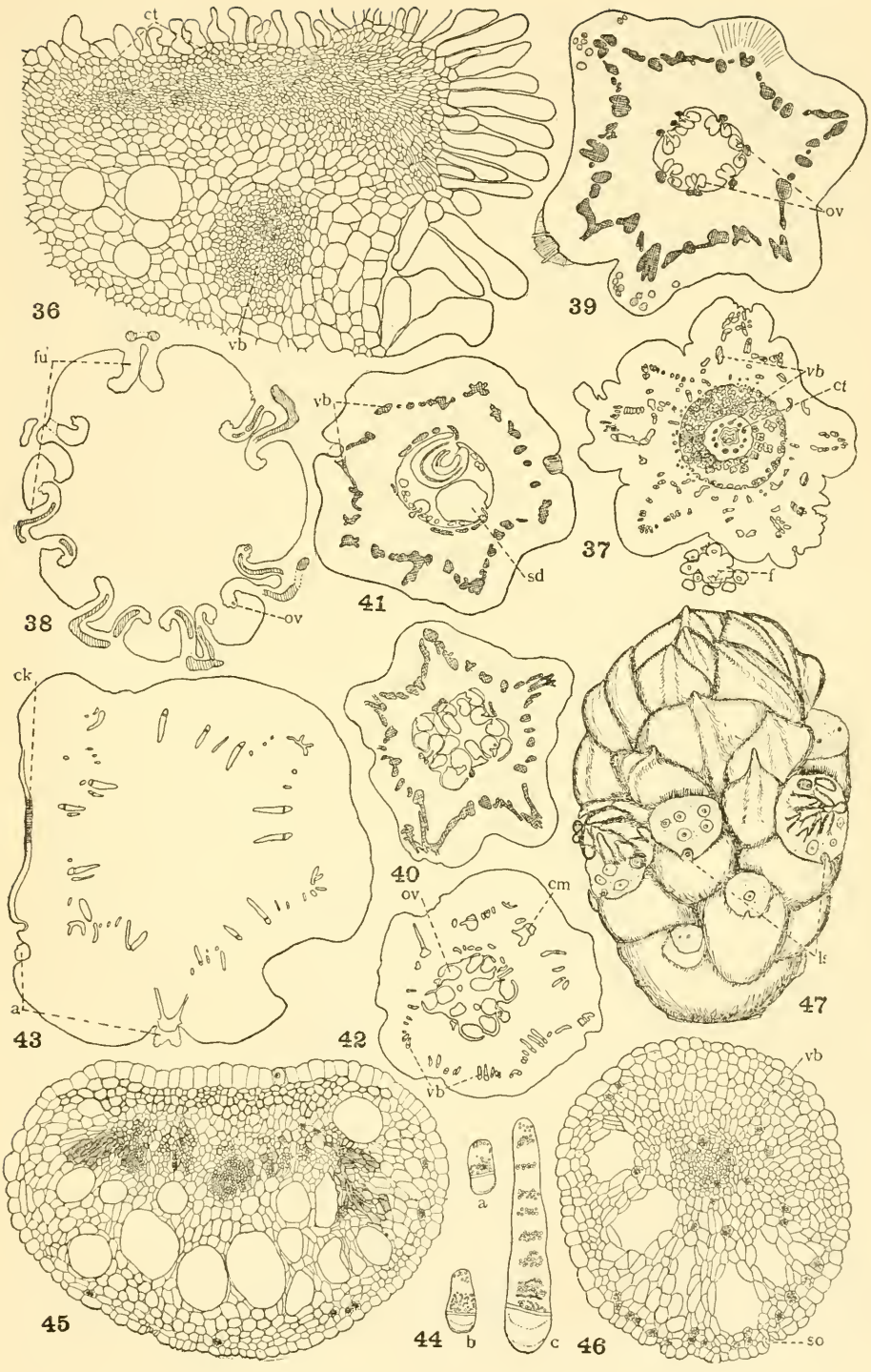
9a

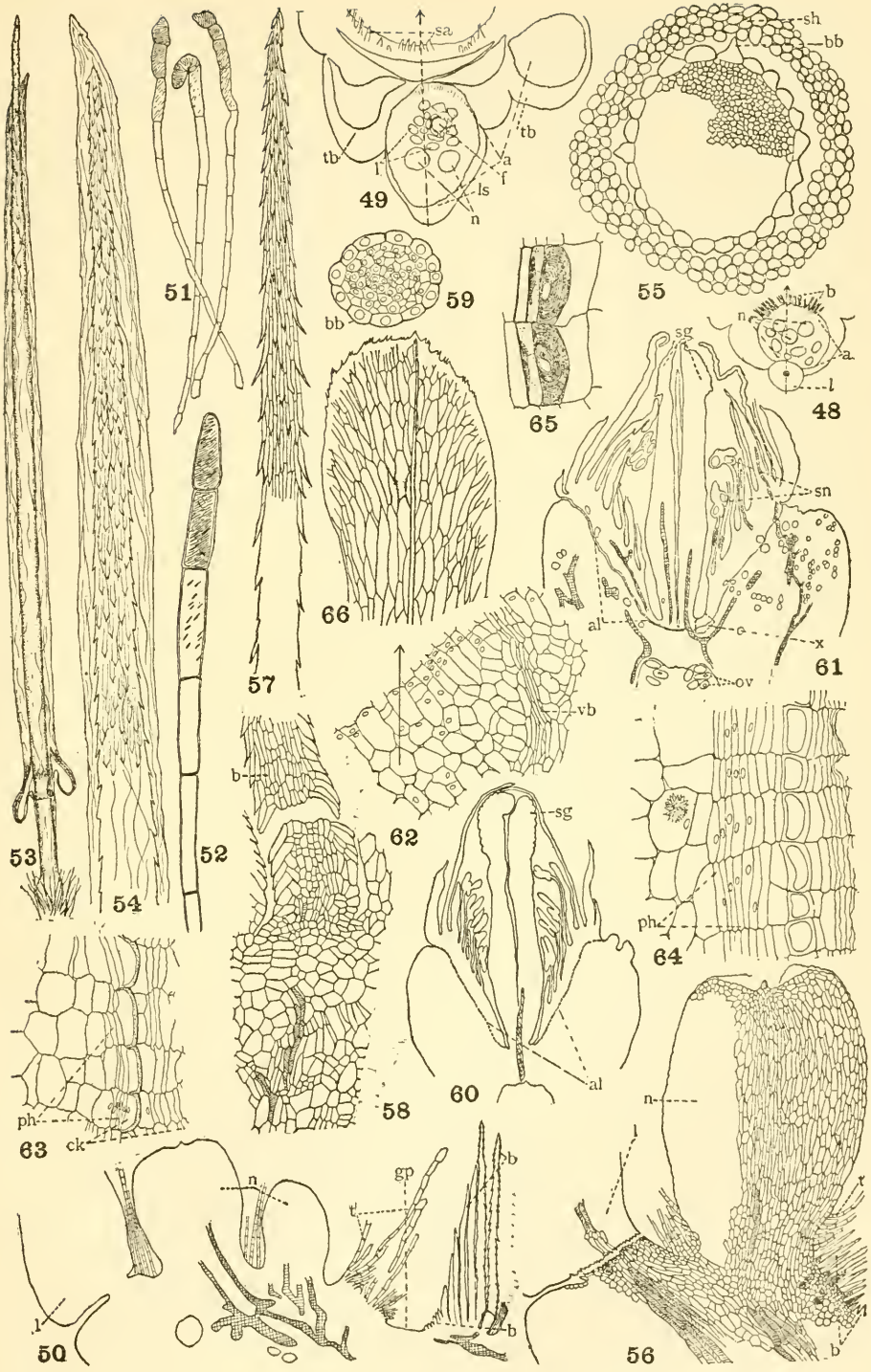
8

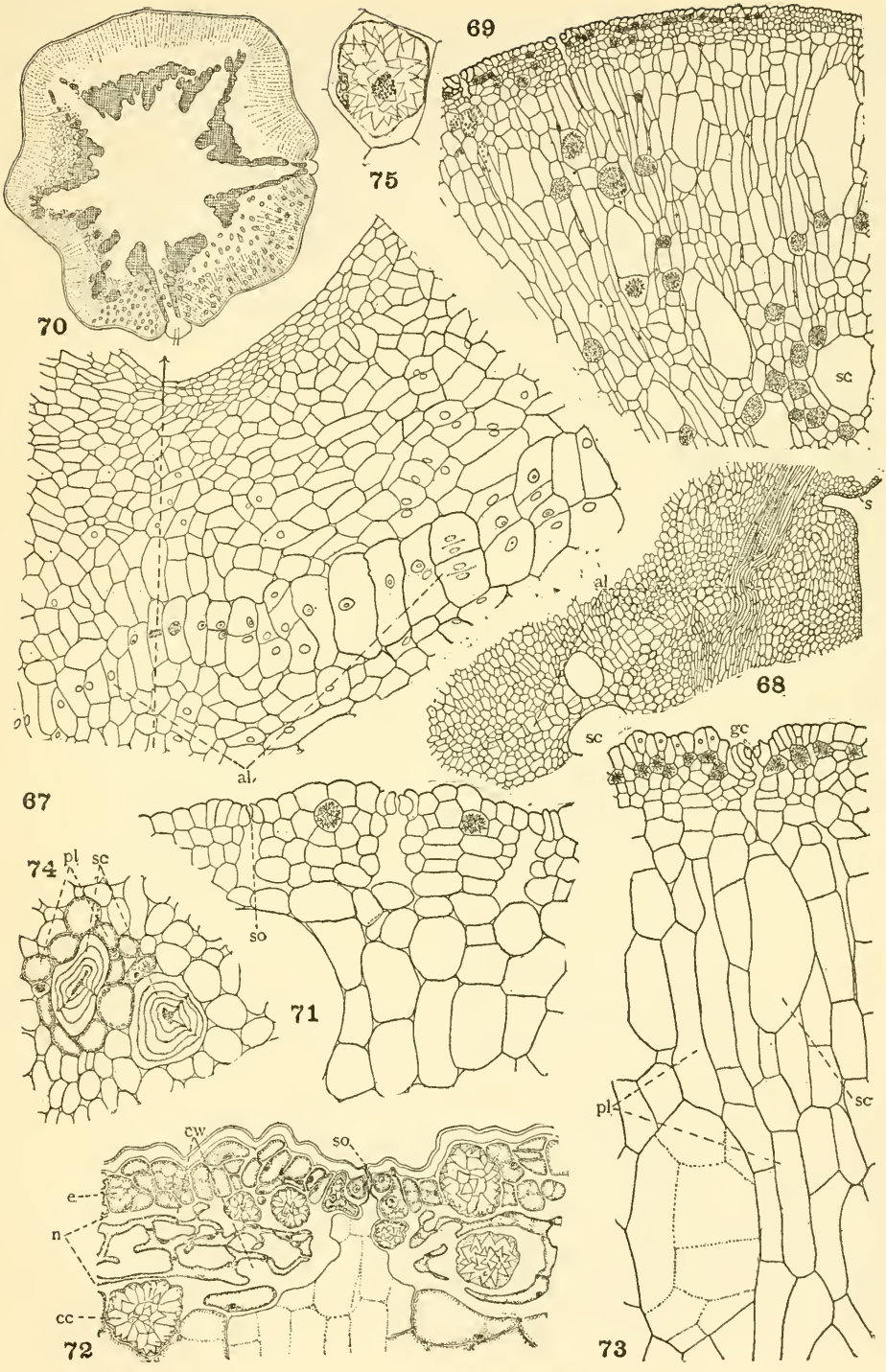
9b


10
l
n
b
s
gp
11
l
n
12
l
vb
n
st
t
b
13
sg
s
f
sp
sa
l
14
l
n
gp
a
gp
n
ls
f
ck
wf
vb
a
15
l
a
gp
16
t
p
sa
l
t
17
n
a
sa
cp
tb
ck
18
sa
c
19
sa
t
20
l
n
ls
a
sa
c
ov
21
sp
22
p
sg
s
ov


c
ph
e
sg
24
26
sg
vb
25
ck
28
ct
n
23
vb
sa
sg
34
sg
30
l
sp
29
ck
27
tb
l
sp
s
tb
31
vb
ov
b
32
cm
vb
33
ct
35


ct
36
ov
39
fu
vb
38
vb
sd
41
vb
ct
37
f
ck
43
ov
cm
42
vb
40
ls
47
vb
45
a
b
c
44
so
46


sa
tb
tb
l
a
f
ls
n
49
sh
bb
55
51
59
bb
65
b
n
a
l
48
sg
sn
66
57
al
e
x
ov
61
vb
62
b
sg
53
54
52
64
ph
ph
63
ck
58
60
al
n
gp
t
b
b
l
50
n
l
r
b
56


69
sc
75
70
s
al
68
sc
gc
67
al
74
pl
sc
so
71
pl
sc
cw
so
e
n
cc
72
73

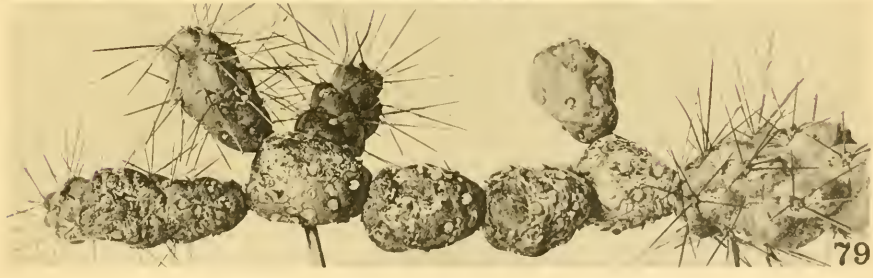
76

80

77

78

81

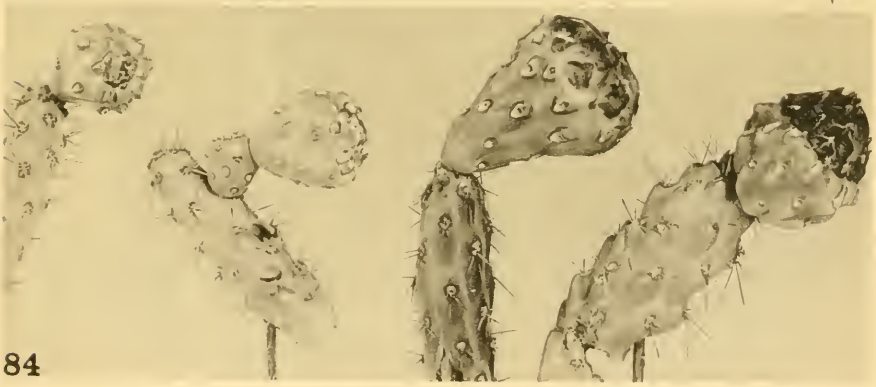

79

85

83

86

82


84

87

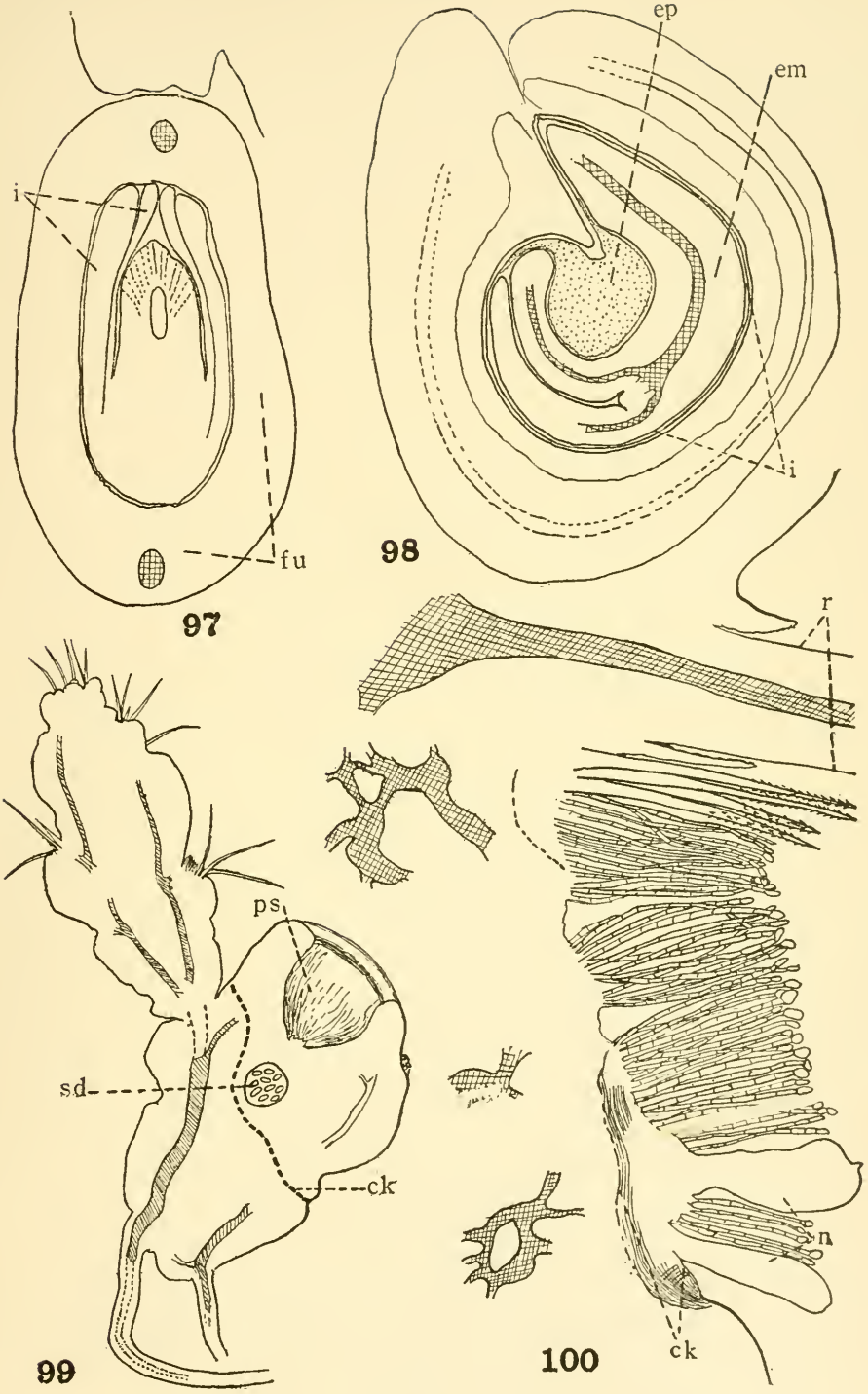
88

89

90

91

93
92
96
95
94


i
fu
97
ep
em
i
98
r
ps
sd
ck
99
n
ck
100